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Space-time heterogeneity in the recovery after experimental burning and cutting in a *Cistus laurifolius* shrubland

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Abstract

Recovery after experimental burning and cutting in a shrubland of *Cistus laurifolius* in NW Spain has been studied. The community was homogeneous prior to the disturbances, and tended to recover through a process of autosuccession. It was tested whether in a small space (two 100 m^2 plots) there was a greater similarity among individual subplots (1 m^2) in five consecutive years, or among the five subplots considered in each plot in the same year. By comparing space and time beta diversity using analysis of variance, no significant differences were observed, which indicates that temporal changes are not of a greater magnitude than space heterogeneity, even on such a small scale. Changes in time are characterized by an increase in cover by woody species, mainly *Cistus laurifolius,* or a decrease in the diversity and richness of species. Space heterogeneity (differences between subplots) does not seem to be determined by environmental gradients, since the sampling surface is very small, and may be due to the effect of some annual or perennial species, which are not dominant and only appear in some subplots, probably due to random dispersal.

Introduction

Mediterranean ecosystems are characterized by great resilience to disturbances, both natural and caused by man (Dell et al. 1986). They often recover through an autosuccession process (Hanes 1971), in which the species appearing immediately after the regressive impact are the same which existed previously (Biswell 1974; Calvo et al. 1992; Casal et al. 1990; Fox & Fox 1986; Gill 1981; Mazzoleni & Esposito 1993; Naveh 1975; Tárrega et al. 1995; Trabaud 1987a). They regenerate from underground organs which managed to survive, or from seed banks in the soil.

Cistus communities are one of the most characteristic ecosystems of the Mediterranean area which spread and maintain themselves due to fire. *Cistus* species were defined by Kuhnholtz-Lordat (1938) as the typical example of social pyrophyte, i.e. pioneer plants spreading by seed and forming dense stands after fire. Nowadays it is thought that they are not only associated to fire, but are heliophytic pioneer species, colonising disturbed areas, free of aggressive competitors (Trabaud 1987b, 1995), even though the rise in temperature during fires favours germination of their seeds (Alonso et al. 1992; Corral et al. 1990; Santiesteban et al. 1993; Thanos & Georghiou 1988; Trabaud & Oustric 1989; Valbuena et al. 1992).

The Mediterranean landscape is also characterized by its diversity and heterogeneity (Trabaud et al. 1993), mainly due to the superposition of impacts which are almost always caused by man. This man- maintained equilibrium has shaped the Mediterranean plant communities into a mosaic of innumerable variants of different degradation and regeneration stages (Naveh & Lieberman 1990). However, observations of the spatial structure may be strongly scale-dependent (Lavorel et al. 1991). Sometimes, there is a microheterogeneity in the vegetation that could be related to the dispersion traits of plants, which condition a great variability on a small-scale on soil seed bank. On the other hand, several authors pointed out that fire acts as an additional source of heterogeneity, e.g. when burning with different intensities occurs or when there is an uneven dispersion of ash which conditions differences in the availability of nutrients (Anderson 1982; Kutiel & Shaviv 1990; Tárrega & Luis 1987). The problem of scale, both of space and time, in diversity patterns is largely discussed by Rosenzweig (1995).

In this study we try to analyze the extent of spatial heterogeneity by comparing spatial with temporal changes in a process of secondary succession after disturbances. A community dominated by *Cistus laurifolius* which was very homogeneous, although small in extension, was chosen. The aim was to determine whether the spatial heterogeneity in an initially uniform community and in a reduced space (100 m^2) surpassed or not the temporal heterogeneity, i.e. the changes after disturbances, taking into account the tendency to recover through autosuccession in these communities. The main structural and floristic changes in the course of time were analyzed and the variabilities in time and space were compared using beta diversity (heterogeneity). We also tried to establish whether the tendencies are similar after two types of disturbances, both normal in this type of ecosystem, burning and cutting of the woody species. This knowledge might be important for the maintenance of biodiversity in Mediterranean ecosystems.

Material and methods

Description of the plots and sampling method

The study was carried out in a shrubland situated in the southwest of the province of León (NW Spain) (M.T.U. 29TQG3929). The altitude was about 900 m. A uniform shrubland was chosen, in which *Cistus laurifolius* was clearly dominant, with an average cover higher than 75%. Other shrub species, although in lower abundance, were: *Chamaespartium tridentatum* (average cover less than 8%), *Adenocarpus complicatus* (less than 4%), *Halimium umbellatum* (2%) and *Cistus ladanifer* (1%). Herbaceous species were scarce, and their average cover was less than 1%. The climax community in this area is a *Quercus pyrenaica – Quercus ilex* forest.

Two plots of 100 m^2 each, with a 2 m wide corridor in-between were established. In each plot the following treatments were applied: cutting the woody species using a mechanical cutter and pruning scissors, and burning the aerial biomass by simulating a wildland fire. Vegetation was surveyed before the start of the treatments to know the original conditions. The experimental treatments took place in July 1989.

The changes in the vegetation community were surveyed annually, from 1990 to 1994. The samplings were carried out in June. At every sampling period, 5 subplots of 1 m^2 per plot (called A, B, C, D, and E), randomly selected and marked the first year, were analysed, recording all species present, the cover in vertical projection of each species, and the percentage of bare soil.

Data analysis

A regression analysis was carried out in order to show the influence of the dominant woody species *(Cistus laurifolius)* on the cover of herbaceous species.

The diversity (H'), using the Shannon index (Shannon & Weaver 1949), and its two components, richness (S = species number) and evenness ($J' = H'/H'\text{max}$) (Pielou 1966), were calculated. The diversity, richness and evenness of each subplot in each sampling period were calculated using these indices (H'_α, S_α, y J'_α), using the average values of the five subplots.

Apart from the diversity of each subplot (H'_α), considered in this case as a microcosmic diversity (Whittaker 1972; Blondel 1979), the diversity of each plot in each sampling year was calculated (H'_γ, or macrocosmic diversity), from the joint consideration of the samples carried out in the five subplots. By using the comparison of both types of diversity, beta diversity (H'_β, spatial heterogeneity) was calculated for each sampling year in each plot, using the formula:

$$H'_\beta = H'_\gamma - \frac{\sum H'_{\alpha \text{i}}}{5},$$

where H'_β = spatial heterogeneity, H'_γ = diversity of the five subplots in each plot (A, B, C, D, and E) in each sampling year, considered as a whole, and $H'_{\alpha\text{i}}$ = diversity of each one of the subplots.

This same formula was applied to the calculation of the beta diversity in time, which measures annual changes (time heterogeneity). In this case H'_β = time heterogeneity, H'_γ = diversity of the five samplings (from the first to the fifth year after the disturbances) of each subplot, considered as a whole, and $H'_{\alpha\text{i}}$ = Diversity of each one of the subplots.

In the first case spatial heterogeneity values were obtained (with regard to the five subplots) in each sampling year (1990–1994), in the second case the temporal variability of each subplot (A, B, C, D, and E) in a five years period.

In order to determine whether the similarity among subplots in the same year differs from that among

Table 1. Alfa diversity (values in the inventories carried out in each subplot throughout the study period) and gamma and beta diversity (heterogeneity) in time and space

		Years after treatment					H'_γ in	H'_β in
		1	2	3	4	5	time	time
CUT PLOT:								
Subplot	A	2.36	2.89	2.65	1.77	1.49	2.71	0.48
	B	2.27	3.52	2.45	1.69	1.66	2.65	0.33
	C	3.17	2.18	1.98	1.75	1.84	2.32	0.14
	D	2.18	3.00	2.14	1.52	1.27	2.55	0.53
	E	1.80	2.25	1.35	1.12	0.73	1.95	0.50
H'_γ in space		2.71	3.13	2.41	1.93	1.74		
H'_β in space		0.35	0.36	0.30	0.36	0.34		
BURNT PLOT:								
Subplot	A	2.44	1.56	1.52	1.36	1.20	1.74	0.12
	B	2.27	1.36	0.83	1.43	1.68	1.67	0.16
	C	2.59	1.59	1.45	1.81	1.75	2.05	0.21
	D	1.85	1.81	1.40	0.66	1.22	1.80	0.41
	E	2.08	2.02	1.87	1.71	1.80	2.31	0.41
H'_γ in space		2.80	1.85	1.59	1.66	1.73		
H'_β in space		0.55	0.18	0.18	0.27	0.20		

samples of the same subplot in consecutive years, a variance analysis was applied, to compare average values of spatial and temporal heterogeneity.

A qualitative TWINSPAN (two-way indicator species analysis) was also carried out on each plot, taking into account only the presence of species, independently of their cover, in order to compare the samples carried out in each subplot in the five years of recovery. In these analyses, species which only appeared in one sample (only in one year and only in one subplot) were not taken into account. TWINSPAN is a method of hierarchical classification which carries out a simultaneous classification of samples and species (Hill 1979).

Results

The analysis of temporal changes in the cover of woody species, perennial and annual herbs reveals that most obvious change consists in the cover increase of woody species (Figure 1). This cover, mainly due to *Cistus laurifolius*, is greater in the burnt plot than in the cut one up to the fourth year, becoming equal afterwards. On the other hand, herbaceous cover, both of annuals and perennials, is greater in the first year in the cut plot than in the burnt one; after the second year, however, there does not seem to be any difference.

The increase in *Cistus laurifolius* cover conditions the decrease in herbaceous species cover, as shown in the regression analysis (Figure 2), which is highly significant (99%).

The temporal changes in the average values of H'_α show a trend of decreasing diversity, with the highest value in the first year in the burnt plot and in the second year in the cut plot (Figure 3). Evenness drops very much in the second year in the burnt plot and in the third year in the cut plot, coinciding with the greatest increase in *Cistus laurifolius* cover in each plot; afterwards there are fewer changes. There is a larger number of species in the cut plot than in the burnt one in all sampling years. In both plots, species richness progressively drops from the second year after disturbances.

On analyzing the temporal trends of spatial heterogeneity (H'_β), practically no changes appear in the cut plot (Table 1, Figure 4). However, spatial heterogeneity is higher in the burnt plot in the first year, decreasing in the second year and maintaining itself without any great changes in the following years, with lower values

Table 2. Two ways analysis of variance for space heterogeneity (beta diversity values in space throughout the five years of sampling) vs. time heterogeneity (beta diversity values in time in the five subplots) in the cut and burnt plots

Two factor analysis of variance				
Source:	df	Mean square	*F*-test	*P* value
Space-time (A)	1	0.002	0.112	0.741
Treatment (B)	1	0.050	2.811	0.113
AB	1	0.006	0.325	0.577
Error	16	0.018		

Mean values			
Treatment	Cut	Burnt	Totals
Space-time			
Year (space)	0.342	0.276	0.309
Subplot (time)	0.396	0.262	0.329
Totals	0.369	0.269	0.319

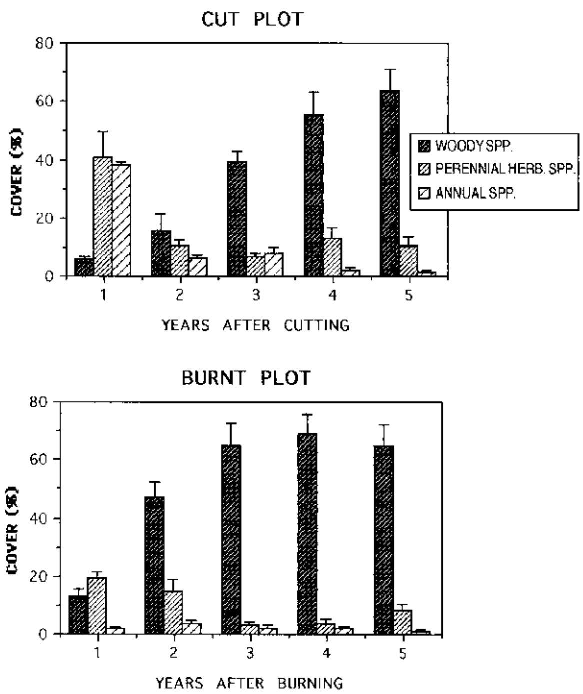

Figure 1. Mean values and standard error of cover of woody species, perennial herbaceous species and annual species in the experimental plots throughout the study period.

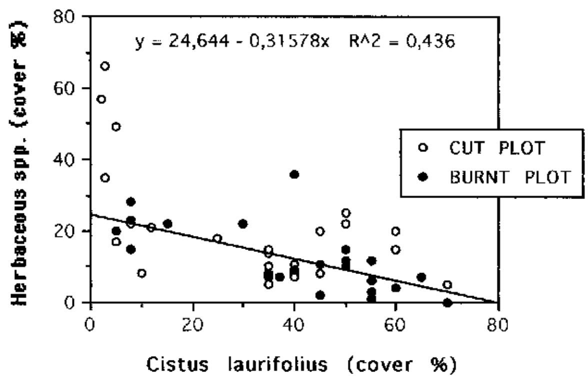

Figure 2. Simple regression analysis between *Cistus laurifolius* cover and cover by herbaceous species in the inventories carried out in the subplots throughout the study period ($p < 0.001$).

than those in the cut plot. The greatest value in the first year after burning confirms the effect of fire as a generator of heterogeneity on a small scale. On the other hand, taking into account the changes in time (H'_β in the time) which each subplot undergoes, no tendencies appear except that, in general, temporal changes are fewer in the burnt plot than in the cut plot. Some subplots, such as A, B and C of the burnt plot and C of the cut plot, show few changes in the five sampling years, while these are somewhat higher in the remainig subplots.

When the changes in heterogeneity in space and time are compared in each plot using analysis of variance (Table 2), no significant differences are detected, with the average value of H'_β being even lower in time than in space in the burnt plot. Comparing the effects of cutting and burning it is not possible to detect signi-

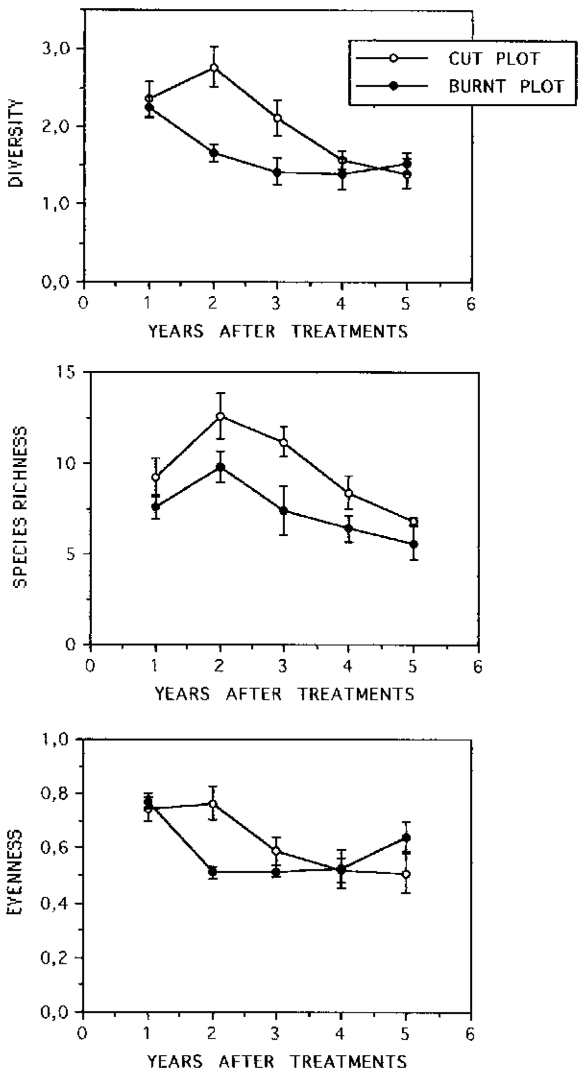

Figure 3. Variation in alfa diversity, species richness and evenness in the experimental plots throughout the study period (Mean values and standard error of the inventories in the five subplots in each plot).

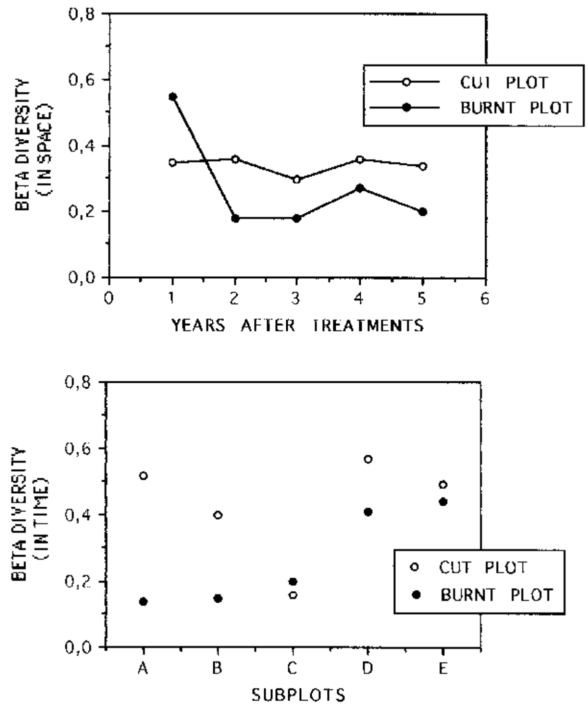

Figure 4. Variation of beta diversity (heterogeneity), in space throughout the study period and in time throughout the subplots, in the experimentla plots.

ficant differences between both plots, even though the average heterogeneity, both in space and time, is lower in the burnt plot.

In the TWINSPAN corresponding to the cut plot, 25 samples (5 subplots sampled 5 years) and 28 species were considered after disregarding the nine species which only appeared in one sample (five of which appeared in the first two years and another two in the third year). The two main groups formed in the first division do not establish a division with regard to recovery time from the cutting (Figure 5), which indicates that the sequential floristic relay described by the classical theory of succession, is not produced. There is one group of species (from *Hypochoeris radicata* to *Rubus ulmifolius),* which only appears in the samples of the first group, while *Chamaespartium tridentatum* and *Arenaria montana* only appear in the second group. A tendency towards association can be observed, although with exceptions, in the samplings of subplots A, B and C, on one hand, and D and E, on the other. *Muscari comosum,* indicator species of the group made up of B1, C2, C1, ... A1, A2, only appears in subplots A, B and C but never in D or E. On the other hand, there are several species which only appear in certain subplots, such as *Cerastium glomeratum* (in subplot A, from the first to the fourth year after cutting), *Rubus ulmifolius* (only in C, from the first to the fourth year), *Cistus ladanifer* (in C, from the second to the fifth year), *Sanguisorba minor* (in all samples of subplot D), etc.

In the TWINSPAN corresponding to the burnt plot, 25 samples and 22 species are considered (after disregarding eight species which only appear once; seven of them occur sporadically in the first three years after burning). As in the cut plot, the groups do not separate the samples with regard to time from disturbance,

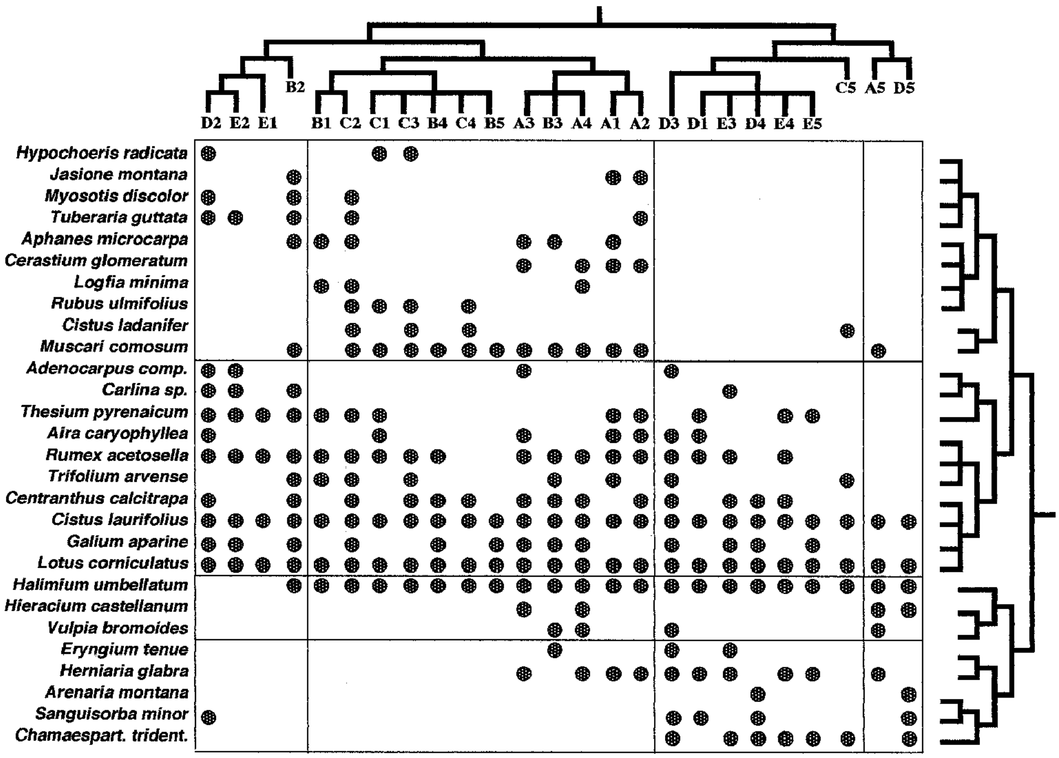

Figure 5. TWINSPAN dendrograms of samples and species for the cut plot. Species presence in each sample is indicated by a point. (The letters A, B, C, D and E indicate the subplots. The numbers after the letters indicate years after cutting.)

with the tendency, although with exceptions, to the association of samples of the same subplot being more clear (Figure 6). The first group, which includes all the samples of subplot E as well as three of subplot D and C2, is associated to species such as *Andryala integrifolia, Veronica verna, Sanguisorba minor* and *Ornithopus compressus,* which appear almost exclusively in subplot E, or *Galium aparine,* which appear in D and E. Other species, such as *Lavandula stoechas* and *Chamaespartium tridentatum,* mainly appear in subplot C, while *Rubus ulmifolius* appears in A and B, conditioning the formation of the last subgroup of the dendrogram of samples.

The most frequent species in both plots are *Cistus laurifolius,* which appears in all samples, *Halimium umbellatum* and *Lotus corniculatus.*

Discussion and conclusions

The temporal changes after burning and cutting confirm the tendency to autosuccession. Species native to the community appear from the first year after the disturbances, and the last years are better characterized by the disappearance of invading species than by the installation of new ones. These observations coincide with the results obtained by many authors in Mediterranean ecosystems (Calvo et al. 1992; Casal et al. 1990; Mazzoleni & Esposito 1993; Tárrega et al. 1995; Trabaud 1987a, Trabaud et al. 1993). The dominant woody species in the initial situation, *Cistus laurifolius,* tends to recover quickly, determining a decrease in herbaceous species as *Cistus* cover increases. The diversity decreases in the course of time, partly due to the effect of *Cistus* dominance (lower evenness), but mainly due to the decrease in species richness.

Comparing the recovery after both burning and cutting, Casal et al. (1984, 1991) found that fire induces floristic changes, with a temporal peak of diversity, but this does not happen after cutting because no pioneer species appears. This differs from the results found in this study, in which a greater abundance of herbaceous species is observed, at least in the first year, in the cut plot than in the burnt one. Furthermore, a greater diversity and richness of species are observed in the cut plot, although differences tend to diminish in the

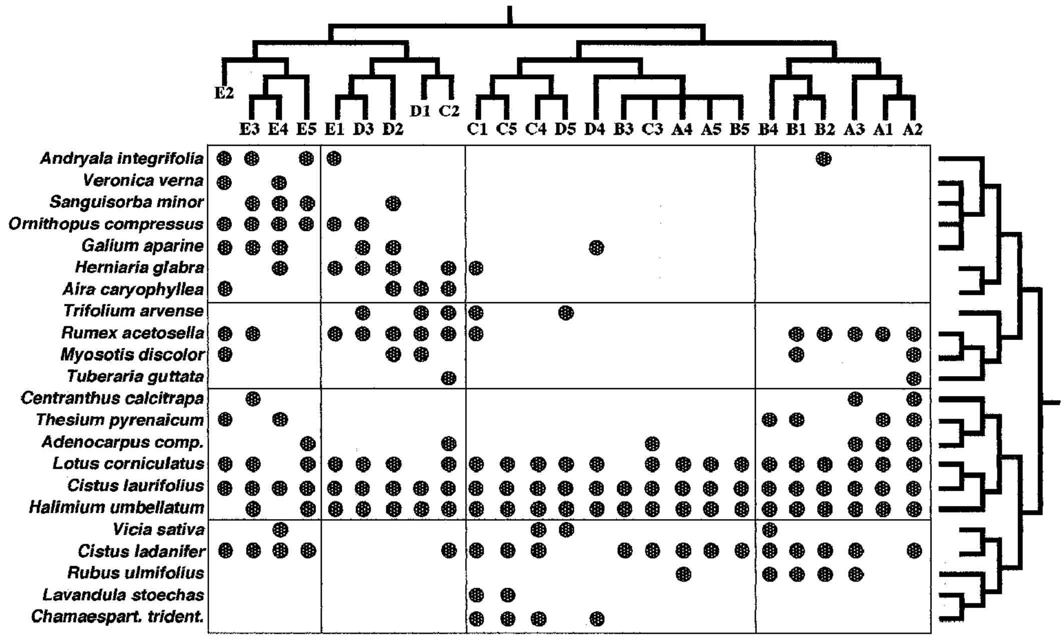

Figure 6. TWINSPAN dendrograms of samples and species for the burnt plot. Species presence in each sample is indicated by a point. (The letters A, B, C, D and E indicate the subplots. The numbers after the letters indicate years after burning.)

course of time. This could be due to the faster recovery of *Cistus laurifolius* in the burnt plot, which inhibits the proliferation of herbaceous species. For this reason, the changes in time are fewer after burning than after cutting, and also spatial heterogeneity, except for the first year after the fire. However, the general tendency to recover is similar in both plots.

The floristic changes are of little magnitude both in time and in space, since a homogeneous community was considered, which recovers by autosuccession. However, given the proximity of subplots, it would be expected that changes in the 5 years of recovery surpass spatial heterogeneity, but this does not happen. In contrast to the temporal changes, those in space do not show clear trends since, in such a small space, the conditions are uniform without noticeable environmental gradients. Spatial heterogeneity is probably due to the random effect and to the capacity of dispersion by the species.

The species which appear in a certain subplot only, could come either from individuals which were already present in the subplot before the disturbances, and which are capable of vegetative resprouting, from the seed bank in the soil, or from seeds which arrive from nearby areas. This third possibility is perhaps the least probable, as it implies that these species have a medium or high dispersion capacity, and hence it would be logical that later on they would spread to other subplots. Although some of the species localized in one or a few subplots, such as *Chamaespartium tridentatum,* can resprout vegetatively, the individuals found came from seedlings. Thus, it is most probable that in most cases they come from the soil seed bank, which is usually characterized by its great variability on a small scale (Bigwood & Inouye 1988; Lavorel et al. 1991), in part as a result of the dispersion traits which tend to concentrate the seeds to a short distance around the mother plant.

Among the very localized species, there are some woody species, such as *Rubus ulmifolius, Chamaespartium tridentatum* and *Cistus ladanifer,* the last one being frequent in the burnt plot but only appearing in one subplot of the cut plot. There are also perennial herbaceous species, such as *Sanguisorba minor,* and annual species, such as *Cerastium glomeratum, Andryala integrifolia, Ornithopus compressus,* etc. The dispersion traits in most of these species are barochory or autochory, which limit their projection to short distances, as is the case of *Cistus* species (Trabaud 1995; Troumbis & Trabaud 1986). However, other species, such as *Andryala integrifolia,* also show dispersion by anemochory.

On the other hand, Lavorel et al. (1991), comparing three abandoned fields which differing in time since the last ploughing, considered as stages in a successional sere, found that the within-field heterogeneity was smaller than the between-field heterogeneity. The discrepancy with the results obtained in this study can partly be explained because these authors did not carry out a consecutive sampling in the same field, and partly because ploughing constitutes a more drastic type of disturbance than cutting or burning.

The results confirm the spatial heterogeneity associated with most Mediterranean ecosystems (Naveh & Lieberman 1990) and reveal them on a very small scale. This microheterogeneity has important implications in planning sampling designs for ecological studies, an aspect also pointed out by Lavorel et al. (1991). In the case of studies on secondary succession after disturbances, the diachronic method (sampling in consecutive dates to follow the changes in a same area, using permanent plots) is more appropriate than the synchronic one (comparing the areas which have undergone the same disturbance at different times), since using the latter the successional changes could be masked by spatial variability.

References

Alonso, I, Luis, E. & Tárrega, R. 1992. First phases of regeneration of *Cistus laurifolius* and *Cistus ladanifer* after burning and cutting in experimental plots. Int. J. Wildland Fire 2(1): 7–14.

Anderson, S. H. 1982. Effects of the 1976 Seney National Wildlife Refuge wildfire on wildlife and wildlife habitat. U.S. Department of Interior. Fish and Wildlife Service. Resource Publication 146. Washington D.C.

Bigwood, D. W. & Inouye, D. W. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. Ecology 69(2): 497–507.

Biswell, H. H. 1974. Effects of fire on chaparral. Pp. 321–364. In: Kozlowski T. T. & Ahlgren C. E. (eds), Fire and Ecosystems. Academic Press. New York.

Blondel, J. 1979. Biogéographie et écologie. Masson, Paris.

Calvo, L., Tárrega, R. & Luis, E. 1992. The effect of human factors (cutting, burning and uprooting) on experimental heathland plots. Pirineos 140: 15–27.

Casal, M., Basanta, M. & García-Novo, F. 1984. La regeneración de los montes incendiados en Galicia. Ed. Univ. de Santiago de Compostela.

Casal, M., Basanta, M., González, F., Montero, R., Pereiras, J. & Puentes, A. 1990. Post-fire dynamics in experimental plots of shrubland ecosystems in Galicia (NW Spain). Pp. 33–42. In: Goldamer J. G. & Jenkins M. J. (eds), Fire in ecosystem dynamics. SPB Academic Publishing. The Hague.

Casal, M., Basanta, M. & Díaz-Vizcaino, E. 1991. Cambios en la estructura de la vegetación en matorrales perturbados en Galicia y estrategias implicadas. III Jornadas de Ecología Terrestre. León (España). 157.

Corral, R., Pita, J. M. & Pérez-García, F. 1990. Some aspects of seed germination in four species of *Cistus* L. Seed Sci. Technol. 18: 321–325.

Dell, B., Hopkins, A. J. M. & Lamont, B. B. (eds) 1986. Resilience in Mediterranean-type Ecosystems. Dr. W. Junk Publ., Dordrecht.

Fox, B. J. & Fox, M. D. 1986. Resilience of animal and plant communities to human disturbance. Pp. 39–64. In: Dell B., Hopkins A. J. M. & Lamont B. B. (eds), Resilience in Mediterranean-Type Ecosystems. Dr W. Junk Publishers.

Gill, A. M. 1981. Adaptative responses of Australian vascular plants species to fire. Pp. 243–271. In: Gill A. M., Groves R. H. & Noble I. R. (eds), Fire and the Australian Biota. Austral. Acad. Sci. Camberra.

Hanes, T. L. 1971. Succession after fire in the chaparral of southern California. Ecol. Monog. 41: 27–52.

Hill, M. O. 1979. TWINSPAN – a FORTRAN program for arranging multivariate data in a ordered two-way table by classification of the individuals and attributes. Ithaca, N.Y. Cornell University.

Kuhnholtz-Lordat, G. 1938. La terre incendiée. Essai d'Agronomie Comparée. La Maison Carré, Nimes.

Kutiel, P. & Shaviv, A. 1990. Effects of soil types, plant composition and leaching processes on soil nutrients following a simulated forest fire. Proc. Int. Conf. on Forest Fire Research, Coimbra (Portugal), C.03 1–12.

Lavorel, S., Lebreton, J. D., Debussche, M. & Lepart, J. 1991. Nested spatial patterns in seed bank and vegetation of Mediterranean old-fields. J. Vegetation Sci. 2: 367–376.

Mazzoleni, S. & Esposito, A. 1993. Vegetative regrowth after fire and cutting of Mediterranean macchia species. Pp. 87–99. In: Trabaud L. & Prodon R. (eds), Fire in Mediterranean Ecosystems. ECSC-EEC-EAEC, Brussels-Luxembourg.

Naveh, Z. 1975. The evolutionary significance of fire in the Mediterranean Region. Vegetatio 29: 199–208.

Naveh, Z. & Lieberman, A. S. 1990. Landscape Ecology. Theory and Application. Springer-Verlag. New York.

Pielou, E. C. 1966. The measures of diversity in different types of biological collections. J. Theor. Biol. 13: 131–144.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press. Cambridge.

Santiesteban, E., García-Plé, C. & Morey, M. 1993. Dynamics of *Cistus monspeliensis* seedlings after fire. Pp. 193–219. In: Trabaud L. & Prodon R. (eds), Fire in Mediterranean Ecosystems. ECSC-EEC-EAEC, Brussels-Luxembourg.

Shannon, C. E. & Weaver, W. 1949. The mathematical theory of communication. Univ. Illinois Press. Urbana.

Tárrega, R. & Luis, E. 1987. Effects of fire on structure, dynamic and regeneration of *Quercus pyrenaica* ecosystems. Ecol. Mediterranean XIII (4): 79–86.

Tárrega, R., Luis-Calabuig, E. & Alonso, I. 1995. Comparison of the regeneration after burning, cutting and ploughing in a *Cistus ladanifer* shrubland. Vegetatio 120: 59–67.

Thanos, C. A. & Georghiou, K. 1988. Ecophysiology of fire-stimulated seed germination in *Cistus incanus* ssp. *creticus* (L.) Heywood and *C. salvifolius* L. Plant, Cell Envir. 11: 841–849.

Trabaud, L. 1987a. Natural and prescribed fire: survival strategies of plants and equilibrium in mediterranean ecosystems. Pp. 607–621. In: Tenhunen J. D. et al. (eds), Plant response to stress. NATO ASI Series, Vol. G 15. Springer-Verlag. Berlin.

Trabaud, L. 1987b. Fire and survival traits of plants. Pp. 65–89. In: The Role of Fire in Ecological Systems. SPB Academic Publishing, The Hague.

Trabaud, L. 1995. Modalités de germination des cistes et des pins Méditerranéens et colonisation des sites perturbés. Rev. Ecol. (Terre Vie) 50: 3–14.

Trabaud, L. & Oustric, J. 1989. Heat requirements for seed germination of three *Cistus* species in the garrigue of southern France. Flora 183: 321–325.

Trabaud, L. V., Christensen, N. L.& Gill, A. M. 1993. Historical biogeography of fire in temperate and Mediterranean ecosystems. Pp. 277–295. In: Crutzen P. J. & Goldammer J. G. (eds), Fire in the Environment: The Ecological, Atmospheric and Climatic Importance of Vegetation Fires. John Wiley & Sons Ltd.

Troumbis, A. & Trabaud, L. 1986. Comparison of reproductive biological attributes of two *Cistus* species. Acta Oecologica. Oecol. Plant. 7 (21): 235–250.

Valbuena, L., Tárrega, R. & Luis, E. 1992. Influence of heat on seed germination of *Cistus laurifolius* and *Cistus ladanifer.* Int. J. Wildland Fire 2(1): 15–20.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21: 213–251.