Diversity patterns of plant functional types in relation to fire regime and previous land use in Mediterranean woodlands

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Abstract. We explore patterns of diversity of plant functional types (PFTs) in Mediterranean communities subjected to landscape-scale fire disturbances in a mosaic of uncultivated and old fields stands. We use regenerative and growth form attributes to establish two sets of PFTs of perennial species living in shrublands and pine forests of NE Spain. We test the following hypotheses: 1. Fire frequency decreases regenerative PFTs diversity by negatively selecting attributes with low regenerative efficiency. 2. Fire history has more influence on regenerative than on growth form PFTs. 3. The lowest diversity of growth form PFTs will be in old fields without recent fires.

We surveyed stands of different combinations of fire and land use histories. Fire history included areas without fires in the last twenty years (unburned), sites burned in 1982 (1-burned), and sites burned in 1982 and 1994 (2-burned). Land use histories considered terraced old fields, and uncultivated stands on stony soils. We analysed patterns of PFT abundance and diversity at the stand level, and across the landscape (among stands absolute deviations from sample medians of the relative cover of PFTs).

At the stand level, fire had more influence on the diversity patterns of regenerative PFTs than on growth form PFTs. Fire decreased the diversity of regenerative PFTs, due to the elimination of the species without effective mechanisms to post-fire regeneration. This effect was not observed across the landscape, but seeders showed more variation in stands with longer history without fire. Land use contributed to explain the diversity patterns of growth form PFT (i.e. the number of growth form PFTs was lower in uncultivated, unburned sites), but it did not influence regenerative PFTs diversity. Patterns of PFTs diversity reflect the response to ecological processes operating at the landscape level. Overall, regenerative and growth form PFTs appear to be more sensitive to the fire history than to the past land use.

Keywords: Fire disturbance; Functional diversity; Growth form; Mediterranean type ecosystem; Post-fire regeneration; Shrubland.

Abbreviations: PFT = Plant Functional Type.

Nomenclature: Bolòs et al. (1990).

Introduction

The analysis of sets of biological attributes in plants, which derives in plant functional classifications, leads to the identification of specific response groups of species sharing key traits that are believed to reflect ecological constraints at the community level (Lavorel et al. 1997; McIntyre et al. 2001). The use of plant functional classifications has been proposed to describe biological attributes of vegetation in relation to climate (Box 1996; Skarpe 1996; Díaz & Cabido 1997), disturbance regime (Lavorel et al. 1999; McIntyre et al. 1999; Kleyer 1999, Pausas 1999b), land use history (Díaz et al. 1999; Lavorel et al. 1999), global change feedbacks (Woodward & Diament 1991; Chapin et al. 1996), or herbivory (Landsberg et al. 1999; McIntyre et al. 2001). For example, we can designate groups of species (plant functional types in a broad sense, hereafter PFTs) based on regenerative attributes (resprouting ability, clonal spread, seed bank persistence, dispersal mode) associated with a particular disturbance regime (McIntyre et al. 1995). This approach may provide insights in the underlying mechanisms of post-disturbance responses of vegetation. Similarly, a set of PFTs may be defined by attributes related to resource acquisition (for example following growth form typologies) in different productivity conditions or successional stages.

Studies on changes in attribute dominance along environmental gradients are common and have shown that, for example, increasing investment in photosynthesis and growth, short life span and strong seasonal green biomass peaks are associated with higher altitudes in central-western Argentina (Díaz & Cabido 1997), or that herbaceous plants with low morphological plasticity and wide lateral spread are more abundant in disturbed, Mediterranean old fields (Lavorel et al. 1999). There is also a growing interest in the role of functional diversity (value and range of functional attributes) in ecosystem processes (Díaz & Cabido 2001). This diversity of PFTs is highly relevant to predict the response of the community to environmental constraints (Naeem et al. 1999). For

example, the number of species within a given PFT defines its degree of redundancy. An increase in species redundancy improves the reliability of ecosystem functioning (Walker et al. 1999), while a decreasing number of species within a PFT may be an indication of a higher vulnerability of the ecosystem to the processes causing this decrease. However, there is still little interest in the descriptors of diversity of these species groups such as the number of PFTs, the number of species within each PFT, or some type of PFT diversity index. Furthermore, there is not much information about how the processes operating at the landscape level determine patterns of diversity in PFTs.

Fire regime and land use history are two main drivers of landscape structure and dynamics in Mediterranean southern Europe (Rundel 1998). Since the 19th century, important changes in land use have occurred in the region. A peak of farming, grazing and wood collection existed during the transition from the 19th to the 20th century. Throughout the 20th century, continuous migration of people from rural to urban areas caused a massive abandonment of previously cultivated fields in which secondary succession has produced a mosaic of shrublands and forests without active management (Giralt 1990; Debussche et al. 1999). Fuel accumulation in these stands is one of the causes of the increase in wildfires in such areas during the last decades (Moreno et al. 1998). Other causes are related to increasing fire hazard due to changing climate (Piñol et al. 1998), and to an increase of ignition sources (Terradas et al. 1998).

Here we explore patterns of PFT diversity in Mediterranean plant communities subjected to a landscape-scale disturbance – wildfires – in a mosaic of uncultivated and old field stands. We use regenerative and growth form attributes to establish two sets of PFTs (hereafter, regenerative and growth form PFTs, respectively). A large number of studies have considered the mechanisms of regeneration involved in the response of the Mediterranean vegetation to fire regimes (Keeley & Zedler 1978; Gill 1981; Trabaud 1987). Therefore for these communities it is possible to consider groups of species based on response to fire which are defined by regenerative attributes (Pausas 1999a, b). Time since last fire also influences PFT diversity patterns because longer periods of time may allow fire-independent species to establish, and fire-dependent species to become less abundant. However, we do not expect recent fire history to completely erase previous patterns of abundance and diversity in PFT, because in Mediterranean-type ecosystems the post-fire regeneration process is highly dependent on the pre-fire vegetation (Hanes 1971; Trabaud & Lepart 1980; Keeley 1986).

Thus our first hypothesis is that fire frequency reduces regenerative PFT diversity by negatively selecting those attributes which do not ensure population maintenance after disturbance. This effect will appear more clearly within plots and will become less evident at larger scales (among plots) due to the variability of fire characteristics (severity, edge effects, post-fire environmental conditions) (Turner et al. 1994), and to the changes in the species assemblages across the territory.

Our next hypothesis is that regenerative PFT diversity is more sensitive to fire regime than growth form PFTs. Growth form, which is primarily associated to resource acquisition and environmental stress, has also been related to fire response (McIntyre et al. 1995). Fire history influences resource availability. For example, recurrent fires may decrease nutrients in the soil by repeated volatization or post-fire soil erosion (Debano & Conrad 1978; Wells et al. 1979). If we recognize a set of PFTs based on growth form attributes, then, under regimes with high fire recurrence, we can expect a reduction of the presence of attributes associated to a greater resource uptake. In addition, the pulse of resource release occurring immediately after a single fire may favour growth forms characterized by short life span and related attributes.

Our last hypothesis is that the lowest diversity of growth form PFTs will be found in old terraced fields at late successional stages. In cultural landscapes, the past land use also determines the structure of the present vegetation (Compton & Boone 2000). Two ecological processes, productivity and succession, are potentially involved in the differences between vegetation patterns in old abandoned fields versus uncultivated stands. Old cultivated sites are more productive than uncultivated ones because crops were mainly grown on deeper soils, of a natural origin or from terraced constructions, with higher nutrient availability. In addition, time after disturbance has been shorter in burned areas than at unburned sites, and competitive exclusion is expected to be more important in late successional stages (Huston 1994). Overall, we expect the mechanisms proposed to explain species diversity patterns also operate on growth form PFT diversity patterns.

In this study, fire history and past land use can be considered as complex factors. Fire history scenarios include here the number of fires in the last two decades and the respective time since last fire. Specifically, there are: no fires since at least 1976, one fire since 1976 (in 1982), and two fires since 1976 (in 1982 and 1994). The structure and composition of Mediterranean communities, such as the one studied here, recover quickly after disturbance (Keeley 1986; Malanson & Trabaud 1987). However, comparisons with the 2-burned stands (2 yr old) should consider that in this case time since last fire is too short for the development of large, reproductive adult plants for most species. Past land use includes the

agricultural history and productivity differences: abandoned old terraces versus uncultivated slopes. Past land use is also a source of variability at the landscape scale. Therefore, we also examine the effects of the interaction between fire and land use history on PFT diversity. Since the relation between a specific process and the patterns of community variability may be highly dependent on the scale, we consider PFT diversity at two levels: within stands and across the extension of the burned area (i.e. among stands).

More specifically, our aim is to investigate the effects of fire and land use history on (1) the differences between the relative abundance (plant cover) of regenerative and growth form PFTs; (2) the number of species belonging to the different PFTs; (3) the diversity of the regenerative and growth form PFTs within a stand, considered as the number of PFTs and the value of the Shannon (H') index for them, and (4) the diversity of PFTs across the landscape, estimated as the variability of the relative plant cover of PFTs in stands with a common fire and land use history.

Study area and Methods

Study area

The study was performed at Garraf Natural Park, ca. 30 km south of Barcelona. The area (almost 10000 ha) is a karstic massif ranging from sea level to 600 m a.s.l. The climate is typically Mediterranean. Mean annual rainfall is 550 mm, with a pronounced summer drought (ca. 100 mm of rainfall from June to August). Mean annual temperature is 17°C. Mean maximum and minimum temperatures are reached in July (28°C) and January (0.5°C), respectively. The vegetation is dominated by evergreen, sclerophyllous shrublands 1.5 m high and open *Pinus halepensis* forests (Bolós 1962).

In Garraf there are three types of area with respect to recent fire history: (1) small, scattered areas that have remained unburned for at least the last 20 yr ('0-burned'), a 7000-ha area burned in July 1982 ('1-burned'), and finally a 4800 ha area within this larger area that was burned again in April 1994 ('2-burned'). Over many centuries, grazing by domestic livestock, mainly sheep and goats, has been important in the whole area. Cores from ancient lakes have provided charcoal dated to the Middle Ages, which has been attributed to the burning of woodlands in order to increase pastures (Riera-Mora & Esteban-Amat 1994). However, agricultural practices have not been historically intensive in the area because of the dominance of stony soils with superficial limestone bedrock. Scattered farms existed on the bottom of valleys and dolinas. Since the end of the 18th and during the 19th century, vineyards expanded much (Ferrer 1998). Viniculture was largely abandoned in Garraf after the arrival of the phyloxera pest in the 1890s (Giralt 1990).

Sampling and data analysis

An extensive survey of natural vegetation was conducted in Garraf from January to March 1996; 30 10 m × 10 m plots were randomly chosen from a 500 m × 500 m grid map in both the 0-burned and 2-burned areas, and 32 plots in 1-burned areas. Vegetation cover of perennial species in each plot was estimated by the point intercept sampling procedure. We recorded the presence of species every 0.5 m along the four sides of the plot and in a 10-m transect located in the middle of the plot. Thus in each plot 94 point-records were used to estimate the cover of the perennial species. The recent (post-1956) land use history (old fields or uncultivated) of each plot was deduced from aerial photographs taken in 1956. From the total number of plots sampled, 31 were identified as terraced old fields (12 0-burned, 11 1-burned and 8 2-burned plots), and 61 as uncultivated (18 0-burned, 21 1-burned and 22 2-burned).

We considered two sets of PFTs based on post-fire regenerative traits and growth forms, respectively. This is *a priori* selection of simple groups of response attributes based on expert assessment. This approach is appropriate when the aim is to interpret patterns of diversity in groups of species in relation to ecological factors, instead of identifying emergent groups of species or syndromes, which would require a multivariate approach. Each species was referred to one of the regenerative and one of the growth-form PFT categories, following the literature (Cucó 1987; Papió 1994; Bolós et al. 1990) and personal observations (see App. 1).

Regenerative traits included (1) ability to resprout after fire, and (2) establishment of new individuals from seeds after fire. Four regenerative PFTs were considered (Table 1a). Seeders that need fire to recruit are present in other Mediterranean ecosystems but are not found in Garraf.

The growth form PFTs were based on the Raunkiaer (1934) life form system which was modified to include size and type of ramification (McIntyre et al. 1995). Ten growth form PFTs were recognized (Table 1b). For each PFT set, we calculated the relative plant cover of each PFT and the number of species within each PFT. The total number of PFTs and the H' diversity index of PFTs were also calculated for each stand from the cover estimations.

The H' diversity index was calculated for regenerative and growth form PFTs as

$$H' = -\sum p_i \log_2 p_i, \tag{1}$$

p_i being the sum of the relative plant cover values for species belonging to PFT i.

Table 1. a. Regenerative and **b.** Growth form PFTs.

a.	
Resprouters	Resprouting after fire; not germinating
Seeders	Germinating after fire, not resprouting
Resprouter-seeders	Resprouting and germinating
Non-regenerators	Neither resprouting nor germinating after fire
b.	
Trees	Single-stemmed macrophanerophytes with persistent buds > 200 cm above ground surface
Large shrubs	Multi-stemmed macrophanerophytes with persistent buds > 150 cm above ground surface
Small shrubs	Multi-stemmed nanophanerophytes with persistent buds < 150 cm above ground surface
Palms	
Vines	
Erect chamaephytes	With most shoots growing erect > 20 cm above ground level
Flat chamaephytes	With most shoots growing parallel to the ground surface, < 20 cm above ground level
Large grasses	Tussock grasses with leaves growing > 50 cm above ground level
Small grasses	
Geophytes	

We used a multivariate analysis of variance (MANO-VA) to investigate if fire history and land use globally influenced the diversity (number of species) and abundance (relative plant cover) of the PFTs. Multivariate analysis provide some information which is not available if each dependent variable (i.e. PFT) is analysed separately, that is, there may be differences among treatments which are not the result of any one dependent variable, but of the whole suite of variables (Scheiner 1993). In our case, we may not obtain significant effects for each PFT separately (ANOVAs), but they can be detected when considering the overall change of the PFTs (MANOVA). In the MANOVA analysis, we excluded one of the PFTs in order to avoid linear combinations of relative plant cover. This multivariate test was complemented by ANOVAs for each PFT to investigate the effects of fire history and land use on the number of species and the relative plant cover in each specific PFT.

Changes in the total number of the regenerative PFTs and the H' diversity index were analysed by two-way ANOVAs with fire history and land use history as independent variables. ANOVA multiple range comparisons were performed by Fisher's PLSD test (Anon. 1989). Data of all dependent variables were transformed to log (x+1) in order to normalize residuals.

We performed the same calculations for the growth form PFTs, except for the relative plant cover of PFT. In this case, the homeocasticity assumption was violated and non-parametric Kruskal-Wallis tests were performed for fire and land use histories, respectively. Non-parametric multiple comparisons between fire histories were performed following Zar (1996).

The effect of fire and land use history on the diversity of the PFTs across the landscape (that is, the variability among the stands belonging to the same class of fire and land use history) was evaluated for both regenerative and growth form PFTs by a MANOVA in which the dependent variable was the absolute deviation – transformed to log (x + 1) – of the relative plant cover of PFTs from sample medians. The use of deviations from means or medians as dependent variables determines whether samples display significant amounts of variation (Manly 1986). In this case one-way MANOVA with six levels (all combinations of fire and land use) was performed because each plot corresponds to one of the six combinations of fire and land use history. This multivariate test was complemented by one-way ANOVAs for each regenerative PFT to evaluate the effect of fire and land use on the variability among plots of the relative plant cover of each PFT. Deviation from homeocasticity assumptions precluded the application of the parametric test on growth form PFT. Therefore a Kruskal-Wallis test was used for this variable.

All statistic analyses were performed following the SUPERANOVA package procedure (Anon. 1989).

Results

Regenerative PFTs

Relative plant cover of PFTs

The two-way MANOVA showed a significant effect of fire history (Wilks' $\lambda = 0.556$, $p < 0.001$), and no significant effects of the land use history (Wilks' $\lambda = 0.943$, $p = 0.174$) and their interaction (Wilks' $\lambda = 0.877$, $p = 0.084$) on the combined variation of relative plant cover of the PFTs. When considering each PFT separately, the most obvious result of the effect of fire history was the elimination of the PFT represented by

Table 2. Two-way Anova of the effect of fire and land use history on the relative plant cover – after log(x + 1) transformation – of each regenerative PFT.

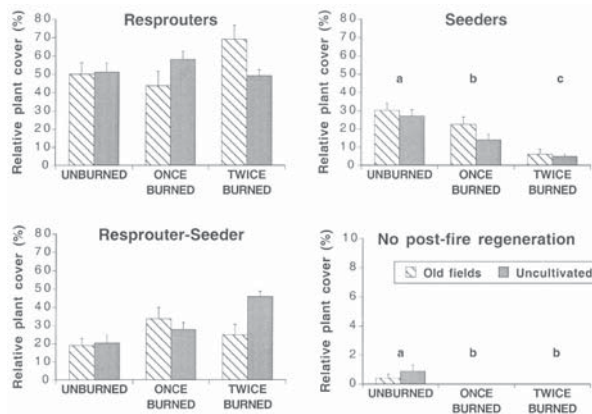|	Fire		Land use		Fire × Land use		Residual
	F	P	F	P	F	P	MS
Resprouters	1.55	0.219	0.01	0.816	4.62	0.012	0.003
Seeders	27.47	< 0.001	2.70	0.104	0.81	0.448	0.002
Resprouter-seeders	6.30	0.003	1.94	0.167	4.16	0.019	0.003
Non-regenerators	6.03	0.004	0.66	0.420	0.68	0.508	< 0.001

Fig. 1. Relative plant cover of each regenerative PFT (mean ± SE) with respect to different fire and land use histories. When the effect of fire history was significant (ANOVA post-hoc Fisher's PLSD test, $p < 0.05$), differences between 0-burned, 1-burned and 2-burned plots are shown by different lower case letters. No significant differences were detected between land use histories. Note the different y-axis scale for non-regenators.

Fig. 2. Number of species of each regenerative PFT (mean ± SE) with respect to different fire and land use histories. When the effect of fire history was significant (ANOVA post-hoc Fisher's PLSD test, $p < 0.05$), differences between 0-burned, 1-burned and 2-burned plots are shown by different lower case letters. No significant differences were detected between land use histories.

the only species, *Juniperus phoenicea*, which does not show any efficient mechanism of regeneration after fire (Riera & Castell 1997). The relative plant cover of seeders also decreased in the 2-burned stands, with no significant effect of land use. Resprouters and resprouter-seeders showed a common pattern: there was no clear trend in their relative cover, with the exception of the increase of resprouter-seeders in uncultivated, 2-burned stands, and of the resprouters in old fields, 2-burned stands, as shown by a significant interaction between fire and land use (Fig. 1, Table 2).

Number of species per PFT

As for the relative plant cover, a two-way MANOVA showed that the effect of fire was significant (Wilks' $\lambda = 0.802$, $p = 0.017$) on the simultaneous variability of number of species per PFT, while the effect of land use was not (Wilks' $\lambda = 0.976$, $p = 0.733$). The interaction between fire and land use history was not significant (Wilks' $\lambda = 0.918$, $p = 0.514$). The number of species per PFT followed the same pattern as their relative plant cover, but no significant differences between fire histories was found in seeder species (Fig. 2, Table 3).
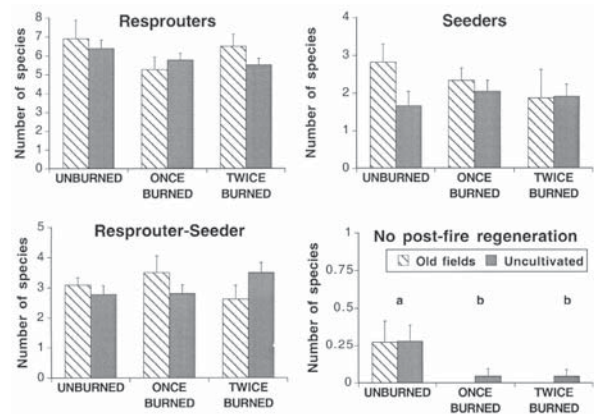
Number of PFTs and Shannon (H') index within stands

Both the number of PFTs and the H' index of regenerative PFTs significantly decreased in burned sites (Fig. 3A, Table 4). However, the effect of land use history and the interaction between fire and land use were not significant.

Diversity of PFTs among stands

The MANOVA results on deviations from median groups indicated that there were not significant differences in the response of regenerative PFTs to the different combinations of fire and land use (Wilks' $\lambda = 0.801$, $p = 0.205$), i.e. the variability among stands was not different as a result of fire and land use history, and diversity across the landscape was not significantly influenced by these factors. When each regenerative PFT was analysed separately by one-way ANOVA, seeders and non-regenerators showed significant differences between combinations of fire and land use (Table 5). In seeders, it was caused by a lower variability among sites in the 2-burned than in the 1-burned and 0-burned stands. As to the non-regenerator type, this was due to the absence of plants in burned stands.

Table 3. Two-way Anova of the effect of fire and land use history on the number of species – after log $(x + 1)$ transformation – of each regenerative PFT.

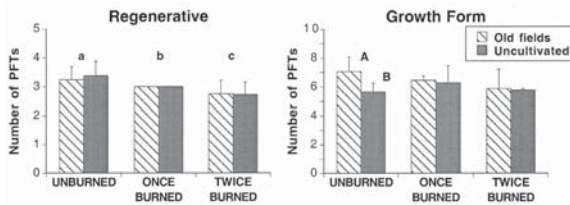|	Fire		Land use		Fire × Land use		Residual
	F	P	F	P	F	P	MS
Resprouters	1.74	0.181	0.06	0.804	1.24	0.295	0.017
Seeders	1.02	0.364	1.81	0.182	1.55	0.218	0.051
Resprouter-seeders	0.01	0.993	0.03	0.873	1.77	0.176	0.026
Non-regenerators	6.43	0.003	0.24	0.625	0.04	0.957	0.008

Fig. 3. Number of regenerative and growth form PFTs (mean ± SE) found with respect to different fire and land use histories. When the effect of fire history was significant (ANOVA post-hoc Fisher's PLSD test, $p < 0.05$), differences between 0-burned, 1-burned and 2-burned stands are shown by different lower case letters. Upper case letters indicate significant differences between land use histories.

Growth form PFTs

Relative plant cover of PFTs

There was a wide variety of responses to the different combinations of fire and land use history. Fire history significantly influenced the relative plant cover of several growth form PFTs (Fig. 4). In four PFTs (trees, small shrubs, geophytes and vines) the relative plant cover generally declined from unburned to 2-burned stands, while in the other two PFTs (flat chamaephytes, large grasses) it increased. Old fields showed significantly higher relative plant cover of small shrubs and vines, whereas uncultivated stands had a higher relative plant cover of large grasses. Among growth form PFTs, the clearer patterns were shown by (1) trees, which dramatically decreased in burned sites, (2) large grasses, which increased in burned sites, especially in uncultivated 2-burned stands, and (3) small shrubs, which increased in old fields, 1-burned stands, but they decreased in old fields, 2-burned stands.

Number of species per PFT

A two-way MANOVA showed significant effects of fire (Wilks' $\lambda = 0.554$, $p < 0.001$) and land use (Wilks' $\lambda = 0.760$, $p = 0.014$) on the number of species within PFT, but not their interaction (Wilks' $\lambda = 0.775$, $p = 0.410$). Fire significantly decreased the number of species of trees, small shrubs, and geophytes, while it increased
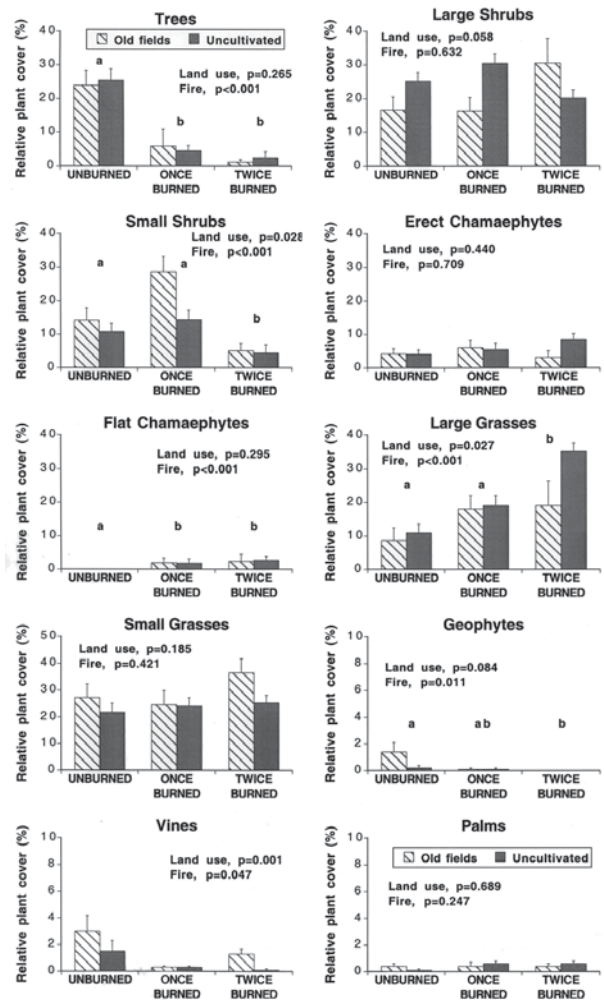

Fig. 4. Relative plant cover of each growth form PFT (mean ± SE) with respect to different fire and land use histories. *P*-values obtained from Kruskal-Wallis tests applied respectively to fire history and land use history are also shown. When the effect of fire history was significant (Non-parametric Kruskal-Walllis, multiple contrast test, $p < 0.05$), differences between 0-burned, 1-burned and 2-burned stands are shown by different lower case letters.

Table 4. Two-way Anova of the effect of fire and land use history on the number and the H' index of regenerative and growth form PFTs – log $(x + 1)$ transformed.

	Fire		Land use		Fire × Land use		Residual
	F	P	F	P	F	P	MS
Regenerative PFTs							
Number of PFTs	14.23	< 0.001	0.35	0.555	0.21	0.809	0.002
H' index	5.32	0.007	0.2	0.653	2.33	0.111	0.005
Growth form PFTs							
Number of PFTs	2.41	0.096	4.93	0.029	2.84	0.064	0.004
H' index	1.96	0.147	0.04	0.843	0.15	0.234	0.002

Table 5. Absolute deviations (mean ± SE) from the medians of the relative abundances of each regenerative PFT in the different fire and land use history stands. One-way Anova results show those PFTs in which significant differences were found. Different letters indicate significant differences (Fisher's Protected LSD test $p < 0.005$) between the respective fire and land use histories.

| | 0-burned | | 1-burned | | 2-burned | | Anova results | |
	Old fields	Uncultivated	Old fields	Uncultivated	Old fields	Uncultivated	F	P
Resprouters	0.178 ± 0.034a	0.163 ± 0.036a	0.234 ± 0.082a	0.155 ± 0.028a	0.168 ± 0.042a	0.107 ± 0.021a	1.47	0.209
Seeders	0.111 ± 0.021a	0.107 ± 0.018a	0.111 ± 0.025a	0.097 ± 0.023a	0.050 ± 0.021ab	0.041 ± 0.011b	2.61	0.030
Resprouter-seeders	0.110 ± 0.022a	0.147 ± 0.026a	0.154 ± 0.037a	0.141 ± 0.022a	0.137 ± 0.027a	0.114 ± 0.017a	0.52	0.756
No post-fire regeneration	0.004 ± 0.003ab	0.009 ± 0.004a	0b	0b	0b	0b	3.37	0.008

the number of species of flat chamaephytes (Table 6, Fig. 5). A significant effect of land use history was only observed in a decrease in the number of vine species in uncultivated stands. In all these cases the pattern was similar to that observed for their respective relative plant cover (Figs. 4 and 5).

Number of PFTs and Shannon (H') index within stands

The number of growth form PFTs exhibited significant differences between land use history categories as a consequence of the lower number of PFTs in uncultivated, unburned stands (Fig. 3B, Table 4). When considering only old fields, there was a marginally significant ($F_{2,28} = 2.90$, $p = 0.071$) decrease in the number of PFTs in burned sites. The H' index for growth form PFTs did not show significant effects of fire or land use history (Table 4).

Diversity of PFTs among stands

The variability among stands of each fire and land use history category, estimated from the MANOVA of the deviations from medians of relative plant cover, was significant (Wilks' $\lambda = 0.871$, $p < 0.001$). When each growth form PFT was analysed separately by one-way ANOVA, significant differences were observed for trees, small shrubs, large grasses, vines and geophytes (Table 7). Trees and geophytes showed a decrease in variability in burned sites. The variability of large shrubs increased in burned sites, particularly in 2-burned stands. Variability in the relative abundance of large grasses also increased in burned sites, especially in uncultivated, 2-burned stands. Vines showed the lowest variability in 1-burned stands (Table 7).
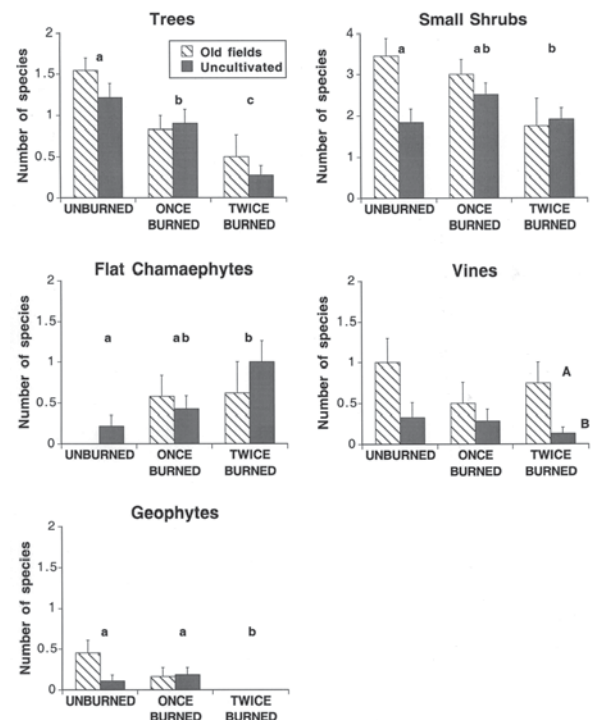

Fig. 5. Number of species of growth form PFTs (mean ± SE) with respect to different fire and land use histories. Only those PFTs in which there was a significant effect of fire or land use history are drawn. When the effect of fire history was significant (ANOVA post-hoc Fisher's PLSD test, $p < 0.05$), differences between 0-burned, 1-burned and 2-burned stands are shown by different lower case letters. Upper case letters indicate significant differences between land use histories.

Table 6. Two-way Anova of the effect of fire and land use history on the number of species (after log(x+1) transformation) of each growth form PFT.

	Fire		Land use		Fire × Land use		Residual
	F	P-	F	P-	F	P-	MS
Trees	15.85	< 0.001	1.50	0.224	0.54	0.582	0.025
Large shrubs	2.25	0.112	3.56	0.063	1.21	0.304	0.023
Small shrubs	4.41	0.015	2.39	0.126	2.85	0.064	0.048
Erect chamaephytes	0.07	0.933	0.09	0.768	0.07	0.931	0.049
Flat chamaephytes	4.88	0.009	0.71	0.401	0.72	0.462	0.035
Large grasses	1.31	0.275	0.08	0.784	0.52	0.595	0.016
Small grasses	1.34	0.267	1.13	0.290	0.79	0.459	0.014
Geophytes	4.67	0.012	2.08	0.152	2.65	0.077	0.010
Vines	1.17	0.315	11.86	0.001	1.15	0.321	0.028
Palms	0.09	0.907	0.45	0.504	0.29	0.747	0.019

Discussion

Fire and regenerative PFTs

As predicted, fire regime had a major influence on the diversity of regenerative PFTs, reducing the presence of species without mechanisms of post-fire regeneration when fires were frequent. This relation was specially evident at the stand level, but not across the landscape, where fire may reduce the variability of the abundance of some regenerative attributes. However, this trend may be counterbalanced by the attribute variability associated to the high heterogeneity of fire severity. We predict that this pattern at the stand level will occur in other Mediterranean-type ecosystems driven by wildfires, but patterns of PFT diversity across landscapes remain to be investigated.

The loss of species without post-fire regeneration mechanisms greatly contributed to the decrease of regenerative PFT diversity at the stand level when fires were frequent. *Juniperus phoenicea* is not able to resprout or recruit after fire, and seedling establishment in periods between fire depends on the arrival of seeds from reproductive *J. phoenicea* adults living in neighbouring, unburned areas. Seeds of this species may be dispersed by vertebrates, but the time since the 1994 fire seems too short to restore populations. Given the large size of the burned area, there is a long distance from seed sources (unburned populations of *J. phoenicea*) in many sites. Our results also suggest that dispersal is ineffective in 1-burned stands. The observed pattern agrees with the reduction of *J. phoenicea* distribution in Garraf documented by Riera & Castell (1997). Therefore, *J. phoenicea* could only establish when long periods between fires occur.

The relative cover of resprouter-seeders increased in burned areas, except in 2-burned, old fields. Fire favours this mixed strategy, as is the case of some Californian species, such as *Adenostoma fasciculatum*, which resprouts and germinates abundantly after fire but rarely establishes by seed in the interval between fires (Zedler 1981). However, the resprouter-seeder species in Garraf were not dependent on fire to recruit, being more similar to the Californian sage-scrub species described by Zedler (1981). Among these species, we find the large tussock grass *Ampelodesmos mauritanica*, which can attain dominance in many stands (Vilà et al. 2001), and several small shrubs such as *Erica arborea*, *Globularia alypum*, and *Dorycnium pentaphyllum*, which regularly produce seedlings in the periods between fires (Lloret 1998).

Table 7. Absolute deviations (mean ± SE) from the medians of the relative abundances of each growth form PFT in the stands with different fire and land use history. One-way Anova results show those PFTs in which significant differences were found. Different letters indicate significant differences (Fisher's Protected LSD test $p < 0.005$) between the respective fire and land use histories.

	Unburned		1-burned		2-burned		Anova results	
	Old fields	Uncultivated	Old fields	Uncultivated	Old fields	Uncultivated	F	P
Trees	0.131 ± 0.019a	0.109 ± 0.023ac	0.055 ± 0.021cb	0.041 ± 0.015b	0.012 ± 0.008b	0.025 ± 0.018b	6.05	< 0.001
Large shrubs	0.091 ± 0.030ac	0.087 ± 0.016a	0.103 ± 0.027ab	0.119 ± 0.015ab	0.176 ± 0.036b	0.153 ± 0.022bc	2.15	0.068
Small shrubs	0.086 ± 0.028a	0.087 ± 0.021a	0.110 ± 0.029a	0.100 ± 0.018a	0.044 ± 0.015ab	0.029 ± 0.005b	3.26	0.010
Erect chamaephytes	0.034 ± 0.011a	0.036 ± 0.011a	0.054 ± 0.017ab	0.045 ± 0.017ab	0.027 ± 0.017a	0.080 ± 0.016b	1.62	0.164
Flat chamaephytes	0a	0a	0.020 ± 0.014ab	0.010 ± 0.004ab	0.024 ± 0.027ab	0.028 ± 0.011b	2.01	0.085
Large grasses	0.071 ± 0.024a	0.105 ± 0.022a	0.119 ± 0.044ab	0.119 ± 0.019a	0.121 ± 0.024ab	0.182 ± 0.022b	2.49	0.037
Small grasses	0.101 ± 0.023a	0.114 ± 0.019a	0.146 ± 0.033a	0.101 ± 0.023a	0.098 ± 0.041a	0.118 ± 0.019a	0.52	0.763
Geophytes	0.014 ± 0.006b	0.002 ± 0.002a	0.001 ± 0.001a	0.001 ± 0.001a	0a	0a	4.98	< 0.001
Vines	0.028 ± 0.009b	0.015 ± 0.008ab	0.003 ± 0.001a	0.003 ± 0.001a	0.010 ± 0.002ab	0.013 ± 0.001a	3.16	0.012
Palms	0.040 ± 0.001a	0.001 ± 0.001a	0.004 ± 0.003a	0.006 ± 0.002a	0.004 ± 0.002a	0.006 ± 0.002a	0.69	0.629

Seeder species significantly decreased in both once and 2-burned areas compared with unburned areas. This pattern may be due to a decline in the number of species, a depressed growth of these species, or a depletion of the seed bank. Probably all three reasons explain the observed pattern. First, the number of species of this group tended to be lower in burned than in unburned sites, although this difference is not significant. Second, seedlings grow slower than resprouting plants after burning. Third, in contrast with other Mediterranean-type ecosystems (Hanes 1971; Zedler 1981), shrub seeders in Northeast Spain (such as *Cistus* spp. and *Rosmarinus officinalis*) do not show a dependence on fire to establish (Lloret 1998; Salvador & Lloret 1995). These species may recruit abundantly after a fire, but short intervals between fires may prevent the achievement of the reproductive stage and the refilling of the seed bank (Trabaud 1987). This may be particularly relevant in the case of the tree *Pinus halepensis*, whose populations need 7 - 10 yr to achieve the reproductive stage (Thanos & Daskalakou 2000). The short time since the last fire surely explains the very low relative cover of trees observed in 2-burned stands. However, the presence of *P. halepensis* is lower both in 1-burned and 2-burned sites (75 and 31% of the stands, respectively) than in unburned sites (97%), indicating that in Garraf the establishment of this species is limited by the short inter-fire interval.

In general, we need to be careful when interpreting diversity patterns in 2-burned areas, where time since last fire may have been too short for the recover of some populations, and where the effects of fire frequency may be confounded by the early successional status. This is particularly important when analyzing patterns of plant cover. Species composition of perennial species is not so sensitive to this confounding effect because it remains quite constant after fire in these Mediterranean communities (Trabaud & Lepart 1980). The simultaneous effect of fire history and successional stage is not so important when comparing 0-burned and 1-burned stands, because 14 yr since the last fire is enough time to regenerate the structure and composition of the community.

In spite of the changes in the relative plant cover of the different regenerative PFTs, the number of species within a PFT was not significantly influenced by fire history (except for the group without post-fire regenerative response). This means that species redundancy within PFT was not diminished by fire, and that potential to recover provided by the species pool remained after this disturbance. This result agrees with the widely recognized high level of resilience of Mediterranean-type communities to fire (Keeley 1986; Malanson & Trabaud 1987).

The overall effect of fire on the diversity of regenerative PFT across the landscape was not significant. However, the variability of the relative plant cover of the different regenerative PFTs was not the same in all fire histories. Apart from the species without post-fire regeneration, which are not present in burned areas, seeders show less variability in 2-burned sites. This pattern may be caused by the lower cover of these species at the first stages of regeneration after fire, particularly in less productive uncultivated sites.

Fire and growth form PFTs

As expected, the effect of fire history on the diversity of growth form PFTs was less important than on regenerative PFTs. Fire history, however, may modify the relative plant cover of some growth form PFTs. This may be the result of dependence between regenerative and growth form PFTs (i.e. many large shrubs such as *Quercus coccifera*, *Arbutus unedo* and *Pistacea lentiscus* are resprouters) (Trabaud 1987). Fire history also determines the successional stage of the community. In particular, large species such as trees are not expected to achieve dominance immediately after fire. Fire recurrence also modifies the possibilities for an abundant species within a certain growth form PFT to achieve reproductive status. For example, the duration of the pre-reproductive period in *Pinus halepensis* is ca. 7 - 10 yr. Fire may also promote the expansion of the tussock-grass *Ampelodesmos mauritanica*, a dominant species within the large grasses group, which vigorously resprouts and reproduces after fire (Vilà & Lloret 2000; Vilà et al. 2001).

However, it is worth pointing out that fire changed the variability of growth form PFTs across the landscape. Particularly, the abundance of large shrubs was more variable in burned sites. Since most large shrubs are resprouters, this result could be related to the influence of fire on the biotic interactions that lead to the dominance of one or few PFTs. Fire produces a temporary increase in resources at the plant level that diminishes competition (Vilà & Sardans 1999), allowing other factors operating at the local scale to become more influential (seed bank, dispersal, founder effect). This may explain the observed variability in the growth form PFTs abundance among sites.

Land use and regenerative PFTs

Land use history did not significantly influence the diversity and the relative plant cover of regenerative PFTs. This trend was also observed in both within- and across-stand diversity, showing that post-fire regenerative mechanisms may be found in different successional

stages or productivity conditions. This pattern concords with the autosuccessional model described for Mediterranean-type ecosystems, in which species composition and structure rapidly recover after fire (Hanes 1971). Trees and shrubs that could be associated with late successional stages can resprout vigorously after fire (Masalles & Vigo 1987), and both seedling establishment and resprouting can be found among small chamaephytes and grasses. Although differences in species composition may be found between old fields and uncultivated garrigues (Bolós 1962), our study shows that the potential to regenerate after fire is basically the same in both community types.

Land use and growth form PFTs

Land use history had more influence on the pattern of the diversity of growth form PFTs than on the diversity of regenerative PFTs. As expected, the lowest growth form PFT diversity was found in unproductive, late successional sites, that is in uncultivated, unburned stands. This pattern implies a significantly marginal interaction between fire and land use. Vines and small shrubs were more abundant in old fields, but with a different pattern in relation to fire history (Fig. 4). Vines included some species with ruderal and invasive characteristics, such as *Rubus* spec., which can be expected to be more abundant in nutrient-rich sites, such as in old fields. This trend increased with time since the last fire. The increase in the relative plant cover of vines in 2-burned, old fields was caused by the resprouting strategy of most of these species after fire. Similarly, small, short-lived shrubs probably found more possibilities to become abundant in productive, disturbed communities, such as burned old fields, where larger shrubs and trees had not yet developed enough to outcompete them. The low cover of this group in 2-burned stands may be related to the seeder regenerative strategy of many of these species (*Cistus* spp., *Rosmarinus officinalis*, *Ulex parviflorus*) and to the small size of the resprouts in the resprouter-seeder species (*Erica multiflora*, *Globularia alypum*). The success of the large tussock grass *Ampelodesmos mauritanica* in 2-burned, uncultivated soils was due to its high ability to resprout (Vilà et al. 2001). Our results suggest that under less productive conditions (shallow soils in uncultivated sites), the post-fire regrowth of *A. mauritanica* was higher than in other species.

Land use history had only a marginal contribution to the pattern of variation of the growth form PFTs across the landscape. Land use only produced a significant effect on the variability among stands in erect chamaephytes living in uncultivated, 2-burned stands, and in geophytes living in unburned old fields. The effect of land use history on the number of species within growth form PFTs also appeared to be negligible. The absence of a clear sequence of substitutions of growth forms along the succession may contribute to this pattern. This may happen when the tolerance mechanism, *sensu* Connell & Slatyer (1977) operates, and the different growth form PFTs are present in the initial composition of the community.

Concluding remarks

Our study reveals that the patterns of abundance and diversity of PFTs are influenced by processes operating at the landscape level. This effect is more evident in those PFTs defined by the response attributes to these ecological processes (i.e. regenerative PFTs are mostly influenced by fire regime). In the Mediterranean communities studied, past land use was evidently less important than fire history in structuring patterns of regenerative PFTs. Since the attributes defining different sets of PFT are not independent, patterns of PFTs may be simultaneously determined by several ecological factors. This is the case for the patterns of growth form PFTs, which are determined by past land use, and to a lower extent by fire history as well. Patterns of PFT diversity may change when considered at different scales. At the stand level, sorting effects due to disturbance or land use history may be more important, while higher variability may exist at larger scales, where other factors, or the own variability of the disturbance regime, also become important.

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