

Predicting the recovery of *Pinus halepensis* and *Quercus ilex* forests after a large wildfire in northeastern Spain

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Received 18 July 2002; accepted in revised form 19 January 2005

Key words: Burn severity, Mediterranean forest, Natural regeneration, Post-fire recovery, Resilience

Abstract

Quercus ilex and *Pinus halepensis* are two of the most common tree species of the western Mediterranean basin. Both species regenerate reliably after fire: *P. halepensis* colonizes recently disturbed areas by effective seedling recruitment, while *Q. ilex* resprouts vigorously after disturbances. For this reason, the natural regeneration of these species after fire should ensure the re-establishment of a forest similar to that which existed before the fire. This study analyzes with a simple simulation model whether or not the relative abundance of monospecific and mixed forests of these species in the landscape is altered by fire. We also analyze the topographic factors and the forest structure before the fire that determine the changes in forest composition after fire. This study has been carried out in a large fire that occurred in NE Spain. Overall, 33% of plots changed to another community type, but this probability of change varied considerably among community types before the fire. Monospecific forests of *P. halepensis* or *Q. ilex* had a high probability of remaining in their original composition after the fire, whereas the resilience of mixed forests of these two species was quite low. Mixed forests changed for the most part to monospecific *P. halepensis* or *Q. ilex* forests. Analysis of several factors determining these changes indicated that only elevation as a significant topographical variable. The effect of fire was to increase the altitudinal differentiation between the two species. *P. halepensis* forests that changed to mixed or *Q. ilex* forests were those of highest elevation, while the mixed and *Q. ilex* plots that changed to *P. halepensis* forests were those located at the lowest elevations. Concerning structural variables before fire, density of *Q. ilex* trees before the fire showed a much greater effect than *P. halepensis* density in determining the post-fire community. Finally, burn severity also influenced the changes observed. For both *P. halepensis* and *Q. ilex* forests, plots that changed to another forest type were mainly those that burned more severely. In the case of mixed forests, even low fire severities involved high probabilities of change to monospecific forests.

Introduction

It is widely accepted that Mediterranean plant communities recover readily after fire; in a relatively short period following a fire, the burned ecosystem cannot be distinguished from the

unburned (Keeley 1986; Trabaud 1987; Ojeda et al. 1996; Arianoutsou 1998). This high resilience to fire is the result of plant life-history adaptations that enable most plant populations to recover fire. Many Mediterranean species recover after fire by resprouting vigorously from protected buds in the

canopy or in the stump (López-Soria and Castell 1992; Moreno and Vallejo 1999) or from germinating seeds stored in the soil or in the crown (Thanos et al. 1992; Keeley 1994; Lloret 1998). Most fire-prone communities include varying proportions of woody sprouters and seeders (Hodgkinson 1998). The efficiency of their regeneration mechanisms is determined both by the state of the community before the fire (Pickett et al. 1987), by fire severity (Hassan and West 1986; Zammit and Zedler 1988; Johnson and Gutsell 1993; Broncano and Retana 2004), and by the physical environment where the disturbance takes place (Callaway and Davis 1993; Turner et al. 1997).

Two of the most common tree species of the western Mediterranean basin are *Pinus halepensis* Mill. and *Quercus ilex* L. Pure and mixed stands of both species dominate extensive areas of the western Mediterranean region (Quèzel and Barbéro 1992; Espelta 1996; Retana et al. 1996) along a gradient determined by topography, climate and time since last disturbance (Retana et al. 1996; Zavala et al. 2000). *Pinus halepensis* density and basal area increase at lower elevations (i.e., in drier and warmer conditions), and *Q. ilex* density and basal area increase at higher elevations (i.e., in wetter and colder conditions). The dynamics of *P. halepensis*–*Q. ilex* forests is mainly determined by fire/post-fire periods, with *P. halepensis* (obligate seeder) dominating post-disturbance conditions, and *Q. ilex* (resprouter) expanding during fire-free intervals (Zavala et al. 2000). *Pinus halepensis* regenerates via seeds guarded in serotinous cones (Saracino et al. 1993; Daskalidou and Thanos 1996; Ariatnoutsou and Ne'eman 2000). *Quercus ilex* is a shade-tolerant, slow-growing species (Mayor and Rodà 1992; Ibáñez et al. 1999) that resprouts vigorously after disturbance (Ducrey and Toth 1992; Giovannini et al. 1992; Espelta et al. 1999), but does not recruit seedlings in the post-fire environment (Retana et al. 1999). Based on the seeding ability of *P. halepensis* and the high resprouting ability of *Q. ilex* after fire, the classical succession theories in the Mediterranean area suggest that it usually takes only before canopy cover recovers after fire (Trabaud et al. 1985; Zavala et al. 2000). Fire disturbance is important in the dynamics of these species (Arianoutsou and Ne'eman 2000; Zavala et al. 2000), but the dynamics of stands

where both species coexist are not well understood.

Here we present the results of a study carried out in an area affected by a large wildfire in NE Spain, mainly covered by monospecific and mixed forests of *P. halepensis* and *Q. ilex* before the fire. Different studies show that the regeneration patterns of these species are not always predictable, either between fires or within a single fire interval (Daskalidou and Thanos 1996; Herranz et al. 1997; Abad et al. 1997; Vallejo and Alloza 1998). The first aim of this study is to analyze, using a simple simulation model, whether or not the relative abundance of the different forest types before the fire in the landscape is altered by fire. The second aim is to determine the main factors (topography, fire severity and forest composition before the fire) contributing to explain the maintenance of the different forest types before the fire or their change to other forest types after the fire.

Methods

Study area

Field sampling was carried out following a large wildfire which occurred in Bigues i Riells (Catalonia, NE Spain) in July 1994 (Figure 1). The fire burned 2692 ha in Els Cingles de Bertí in the Sierra Prelitoral Catalana (Barcelona, Spain; 41°40' to 41°43' N; 2°10' to 2°16' E). The climate is sub-humid Mediterranean (according to the Thornwaite index), with mean annual temperature of 15.2 °C and mean annual precipitation of 625 mm. *Pinus halepensis* and *Q. ilex* were the most abundant tree species. This study was concentrated in the lower elevations (300–700 m) of the burned area, where pure *P. halepensis* forests represented 39% of the total surface, mixed *Q. ilex*–*P. halepensis* forests occupied 56% of the area, and *Q. ilex* was the dominant species in 5% of stands.

Plot sampling

Ninety-three circular plots of 10 m radius were randomly distributed along the study area in spring 1996. The following measures were obtained in each plot:

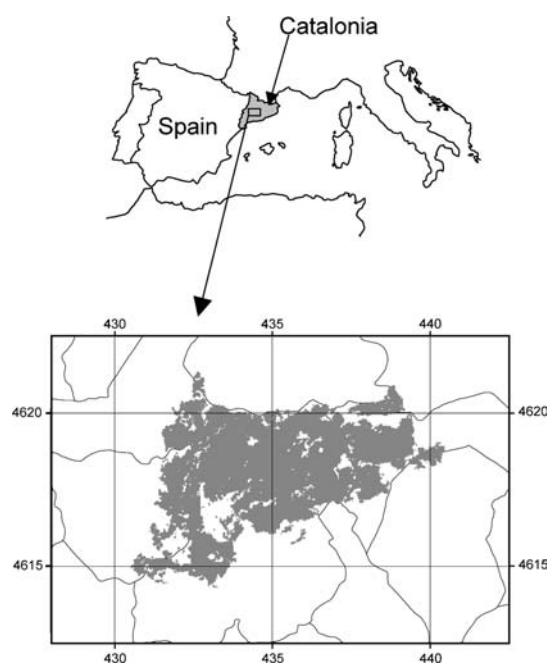


Figure 1. Geographical location of the area burned in 1994 in Bigues i Riells (Catalonia – in gray in the general map –, NE Spain).

- (1) *Topographic features*, including: elevation, slope, and aspect (north, east, south and west, each category of 90°).
- (2) *Forest structure before the fire*. Structural features of the forest before the fire were determined by measuring total tree (individuals with diameter at breast height (dbh) – higher than 5 cm) density of the different species included in the plot. The different species were easily recognized in the plots after the fire.
- (3) *Burn severity*. According to the effect of fire on *P. halepensis* crowns (Broncano and Retana 2004) two types of fires were identified: (a) severe surface burn, where trees were killed but canopy needles were not consumed; (b) crown fire, where canopy needles were consumed; we distinguished two levels of severity for crown fires: light (i.e. trees killed but had fine branches in the whole crown), and severe crown fire (i.e. trees killed without fine branches or only at the top of the crown).

- (4) *Post-fire regeneration*. For sprouting *Q. ilex* stumps, the number of surviving trees per stump and the number of resprouting stumps were counted. The number of *Q. ilex* seedlings before the fire and saplings (i.e. young individuals not reaching the criterion of dbh larger than 5 cm), not included in the previous inventory but that sprouted after fire was also counted. New seedlings of *Q. ilex* and *P. halepensis* established after fire were counted in the whole plot. In 14 of the plots, a total number of 816 *P. halepensis* seedlings were tagged. Seedling survival in these plots was monitored in 1996, 1997, 1998 and 1999 in order to compute the seedling survivorship function described below. Weather was typical during this study period, because rainfall in each of the four sampling years was 884, 628, 580 and 692 mm, values that are included in the interval of 96% (670 ± 328 mm, mean \pm 2SD) obtained for the meteorological station of Centelles (7–15 km away from the burned area; dataset available from 1951 to 2002).

Estimation of the probability of community change

Based on density data of the two species before the fire and the post-fire regeneration data, the probability of community change of the different communities before the fire was determined. Changes were expected to affect vegetation 30 years after fire, which is the period of time required for the canopy to close in Mediterranean forests after disturbance (Trabaud 1994; Espelta et al. 1995). The different community types assigned to each sampling plot were determined according to the relative abundance (in stem density) of the different tree species before the fire. First of all, we distinguished between shrubland and forest plots following the standard criterion of the Forest Ecological Inventory of Catalonia (Gracia et al. 2000). We identified shrubland plots as those having less than 179 trees/ha (in the case of *P. halepensis*) or 271 trees/ha (in the case of *Q. ilex*), which are the densities that correspond to 10% of forest cover for each species. When there were two species in the plot, the weighted value

according to the proportion of each species in the plot was used. Four plots were classified as shrublands.

The other plots were classified in the following forest types:

- Monospecific forests were defined as those with a density of the most abundant species > 66.6% of total tree density. The total number of monospecific plots considered was 58 of *P. halepensis* and 16 of *Q. ilex*.
- Mixed plots were defined as those forest plots with a density of *Q. ilex* and *P. halepensis* higher than 33.3% of total tree density. Fifteen plots were included in this category.

To determine the rate of community change of each forest type, we simulated the densities of *P. halepensis* and *Q. ilex* 30 years after fire using the densities just after fire (measured in the field) and two different vectors:

- Vector of *P. halepensis* seedling survival rates 30 years after fire, i.e. a vector whose entries were the proportion of surviving seedlings per plot, estimated using a survivorship function. Data were obtained in the 14 permanent plots described above. An exponential function was fitted to the data of each plot ($\text{Survival} = 104.5 (\text{Time after fire})^{-0.274}$, $R^2 = 0.86$, $p < 0.001$). This function was used because it showed the best fit to the data and gave similar results to those also reported for *P. halepensis* elsewhere (Papió 1990, Ne'eman et al. 1995, Herranz et al. 1997). The resulting vector of survival rates 30 years after fire was generated from the values obtained with this function in each plot (final range of survival rates 30 years after fire: 0.27–0.53).
- Vector of the number of stems per individual of *Q. ilex* 30 years after fire, i.e. a vector whose entries were the number of stems per individual of 100 individuals in 10 plots in an area burned 30 years ago and located near the study area (final range of number of stems per individual: 1.0–7.2).

The rate of community change for each community type 30 years after fire was computed by running a stochastic simulation model. For each pre-fire community type, one hundred simulations

were performed. In each simulation, the model computes the densities of *P. halepensis* and *Q. ilex* as follows:

- (a) *P. halepensis* tree density. The number of *P. halepensis* trees 30 years after fire was estimated as the initial number of seedlings in the plot multiplied by a randomly-chosen value of the vector of seedling survival rates described above.
- (b) Density of *Q. ilex* stems. Stem density of *Q. ilex* 30 years after fire was calculated considering separately crown-resprouting and stump-resprouting individuals. Crown-resprouting individuals were considered as alive, and their resprouting stems were counted directly as living stems 30 years after fire, because no mortality of adult individuals was assumed. For stump-resprouting individuals, total stem density was calculated as individual (= genet) density after fire times a randomly-chosen value of the vector of number of stems per individual 30 years after fire. As no new *Q. ilex* seedlings were found in the plots, they were not included in the model. Thus, stem density 30 years after fire in each plot was the sum of the number of crown-resprouting stems and the number of stems from stump-resprouting individuals.

The type of community in the plot 30 years after fire is computed from these *P. halepensis* and *Q. ilex* densities as before the fire. In each simulation we computed the proportion of plots that remained in the same forest type before the fire or changed to another type. We carried out one hundred simulations per forest type and, thus, we had one hundred values of probability change of each forest type before the fire to the same or another forest type.

Three assumptions were accepted in the model: (1) no new disturbance would occur during the 30-year period; (2) we assumed that *Q. ilex* individuals that survived fire (either surviving trees or resprouted burnt stumps) had nil mortality during the following 30 years, based on Ibañez et al. (1999) and on the comparison of the Second and the Third Spanish National Inventories in the region of Catalonia (sampled in 1990–1992, and in 2000–2002, respectively); and (3) the incorporation of new recruits after the first regeneration flush was negligible or nil (this pattern has been confirmed for both *P. halepensis* – Daskalidou and

Thanos 1996; Herranz et al. 1997; Thanos 1999 and *Q. ilex* – Espelta et al. 1995).

To explore the sensitivity of the rate of community change to variations of the variables used in the model, separate tests were carried out for the variables used to determine the post-fire community type. In the case of survival of *P. halepensis* seedlings, for each forest type before the fire we have computed simulations of community change 30 years after fire by choosing randomly a value of number of stems per individual of *Q. ilex*, while the value of survival of *P. halepensis* seedlings was established as four different values: mean + 1, + 2, -1 and -2 SD of the distribution of the values registered in the field for this variable. Similarly, we have analyzed the sensitivity of the rate of community change to variations in the number of stems per individual of *Q. ilex* by computing simulations of community change choosing randomly a value of survival of *P. halepensis* seedlings and using the mean + 1, + 2, -1 and -2 SD of the distribution of the values of number of stems per individual of *Q. ilex*. For each of these tests, we have performed 100 simulations for each forest type before the fire. The differences in the rates of community change obtained with these values and those obtained with the model that uses random values of the two variables (survival of *P. halepensis* seedlings and number of stems per individual of *Q. ilex*) showed the sensitivity of the model to variations of these variables.

Data analysis

The variations of different topographic variables (except categorical ones, such as aspect) and variables of forest structure before the fire in plots that changed to different forest types after fire were analyzed using one-way ANOVAs. The type of community in each plot 30 years after fire was computed from the *P. halepensis* and *Q. ilex* densities obtained by multiplying the initial number of seedlings (or number of stump-resprouting individuals in the case of *Q. ilex*) in the plot multiplied by the mean value of the vector of seedling survival rates (or number of stems per individual) 30 years after fire. Data of density of *Q. ilex* and *P. halepensis* before the fire were log-transformed data before the analyses to render them normal and homoscedastic. To compare the number of plots

from the different levels of categorical variables (aspect and burn severity) that changed to different forest types after the fire, different χ^2 tests were carried out separately for mixed plots, monospecific *P. halepensis* plots and monospecific *Q. ilex* plots. We have carried out generalized logistic regression models for post-fire change/not change of *P. halepensis*, mixed and *Q. ilex* plots (dependent variable) considering all topographic, structural and fire variables as independent variables.

Results

Probability of community change

The probability of change varied considerably among community types before the fire (Figure 2):

- The monospecific *P. halepensis* forest showed high stasis, with a 77% probability of remaining as the original type 30 years after the fire. There was a 9% probability of changing to shrubland or mixed forest and 5% probability to changing to *Q. ilex* forest.
- The monospecific *Q. ilex* forest also showed high stasis (68% of remaining as the original type). 23% of plots changed to mixed forest, 8% to *P. halepensis* forest and only 1% to shrubland.
- The mixed forest showed lower stasis, because showed only 29% of plots remained as mixed forest 30 years after the fire. Plots changed for the most part to *P. halepensis* forest (35%) and to *Q. ilex* forest (29%), and only in 7% of cases changed to shrubland.
- Finally, the probability of remaining as shrubland was 54%. 25% of plots changed to *Q. ilex* forest and 21% to *P. halepensis* forest.

The results of the sensitivity analysis of the rate of change to the variations of density of *P. halepensis* seedlings and density of resprouted *Q. ilex* individuals after fire are shown in Table 1. The overall effect of the variations in stems per individual of *Q. ilex* was higher than that in survival of *P. halepensis* seedlings in all forest types before the fire except in the shrubland. The highest variations compared to the values obtained with the random model were observed in the mixed and *Q. ilex* forests.

Factors affecting maintenance of the forest type or a change to other forest types after fire

Some of the topographic variables tested explained in part the changes to other community types after fire (Table 2). There were significant differences in elevation between *P. halepensis* plots remaining the original type and those changing to other forest types after fire. Thus, *P. halepensis* plots that changed after fire were located at higher elevations than those that remained pine forests (535 and 412 m of elevation, respectively). The opposite pattern was found for *Q. ilex* plots (465 and 651 m of elevation, for plots that changed or remained the original forest type, respectively).

Concerning structural variables before fire, *Q. ilex* density before the fire showed a much greater effect than *P. halepensis* density on determining the post-fire community (Table 2). Thus, *P. halepensis* plots that changed had higher density of *Q. ilex* than those that did not change (Figure 3), and also had fewer pines before the fire (594 versus 899 pines/ha). Mixed plots that changed to *Q. ilex* forest also had higher density of *Q. ilex* before the fire than those that changed to *P. halepensis* forest or remained as mixed plots, while *Q. ilex* plots that remained as *Q. ilex* forests were those with higher *Q. ilex* density before the fire (Figure 3). Burn severity also affected the post-fire

composition of monospecific *P. halepensis* and *Q. ilex* plots (Table 2): in both cases, plots that changed after fire burned with greater severity than those that remained as the same type than the one before the fire.

A generalized logistic regression model for post-fire change/not change of *P. halepensis* plots (dependent variable) considering all variables of Table 2 as independent variables included elevation (Wald statistic=4.1, $p=0.040$) and *Q. ilex* density (Wald statistic=4.7, $p=0.029$), but not the other variables ($p>0.1$ in all cases). A similar analysis for mixed or *Q. ilex* plots could not be carried out because of the low number of plots available.

Discussion

Quercus ilex and *P. halepensis* regenerate well after fire, even though they have very different post-fire responses: *P. halepensis* has a notable potential to colonize recently disturbed areas by seeding (Trabaud 1988; Tsitsoni 1997), while *Q. ilex* shows a vigorous resprouting after disturbances (Ducrey and Boisserie 1992; López-Soria and Castell 1992; Espelta et al. 1999), but a limited range of environmental conditions for seedling establishment (Bran et al. 1990; Retana et al. 1999). In this study, in most plots where *P. halepensis* or *Q. ilex* form monospecific stands, they remain the dominant species after fire, although they also show a certain probability to change to other community types (Figure 2). On the contrary, the resilience of mixed forests of these two species was quite low, changing for the most part to monospecific *P. halepensis* or *Q. ilex* forests (Figure 2). There are, however, a proportion of monospecific forest plots that change to mixed plots. In another large fire which occurred in 1994, Espelta et al. (2002) estimated that the surface covered by mixed *P. halepensis* forests decreases after fire. Although *P. halepensis* has been described as an obligate seeder species clearly specialized for fire-prone environments and whose population expansion is dependent upon fires (Trabaud 1987), the results obtained in this study do not suggest that fire favors *P. halepensis* over *Q. ilex*. Thus, mixed forests change to *P. halepensis* forests in a proportion only slightly higher than to *Q. ilex* forests (Figure 2), while the percent of plots that change from *P. halepensis*

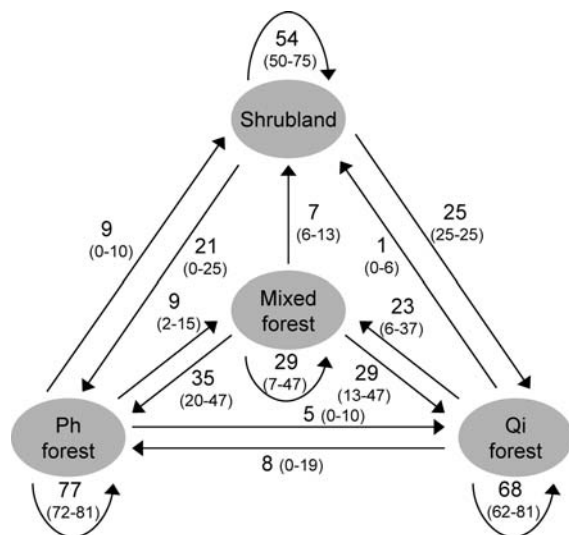


Figure 2. Probability of each forest type before the fire remaining the same or changing to another type 30 years after fire. Ph, *P. halepensis* forest; Qi, *Q. ilex* forest.

Table 1. Sensitivity of the rate of change to the variations of the variables used in the model (density of *P. halepensis* seedlings, and stems per individual of resprouted *Q. ilex* individuals after fire).

Forest type before the fire	Forest type after fire	<i>Pinus halepensis</i> survival				Random model	Stem per individual of <i>Quercus ilex</i>			
		-2 SD	-1 SD	+1 SD	+2 SD		-2 SD	-1 SD	+1 SD	+2 SD
<i>P. halepensis</i>	<i>P. halepensis</i>	73	76	79	80	77	82	81	73	71
	Mixed	11	9	8	7	9	7	8	10	12
	<i>Q. ilex</i>	7	6	4	4	5	0	1	10	10
	Shrubland	9	9	9	9	9	11	10	7	7
Mixed	<i>P. halepensis</i>	24	33	40	44	35	52	45	24	17
	Mixed	30	24	26	26	29	25	28	29	33
	<i>Q. ilex</i>	38	36	26	23	29	10	20	40	43
	Shrubland	8	7	8	7	7	13	7	7	7
<i>Q. ilex</i>	<i>P. halepensis</i>	3	5	8	14	8	30	20	0	0
	Mixed	23	24	23	21	23	8	16	28	21
	<i>Q. ilex</i>	73	70	68	65	68	55	64	72	79
	Shrubland	1	1	1	0	1	7	0	0	0
Shrubland	<i>P. halepensis</i>	0	0	25	25	21	19	20	18	20
	Mixed	0	0	0	0	0	0	0	0	0
	<i>Q. ilex</i>	25	25	25	25	25	25	25	25	20
	Shrubland	75	75	50	50	54	56	55	57	55

For each variable, we have computed simulations of community change by choosing randomly a value of this variable and four values of the other variable: the mean +1, +2, -1 and -2 SD of the distribution of the values registered in the field. The rate of community change obtained with the model that uses random values for the two variables is also indicated in each case. Numbers indicate the percentage of cases ($N=100$ for each forest type before the fire and test) that do not change or that change to another forest type after fire. In bold, values at least 10% higher or lower than the value obtained with the random model.

Table 2. Comparison of topographic variables, structural variables before fire and burn severity between burned plots of the three forest types that remain as the same forest type or change to a different forest type after fire.

Forest type	Variables	Statistical test	<i>P. halepensis</i> forest			Mixed forest			<i>Q. ilex</i> forest		
			DF	F or χ^2	P	DF	F or χ^2	P	DF	F or χ^2	P
Slope	ANOVA	1.56	1.28	0.262	2.10	0.38	0.658	1.14	0.23	0.639	
	χ^2	3	2.82	0.420	6	0.51	0.526	3	3.77	0.288	
Elevation	ANOVA	1.56	14.0	0.001	2.11	1.17	0.344	1.14	22.80	0.001	
	ANOVA	1.56	15.9	0.001	2.11	5.90	0.018	1.14	16.2	0.001	
Adult <i>Q. ilex</i> density (log)	ANOVA	1.56	4.4	0.040	2.11	0.78	0.482	1.14	3.51	0.082	
	χ^2	2	7.4	0.025	4	0.87	0.928	2	8.57	0.035	

In the case of mixed plots, the comparison is carried out among three groups: plots that do not change, plots that change to *P. halepensis* forest, and plots that change to *Q. ilex* forest. The statistical test carried out in each case is indicated. In bold, significant values at $p=0.05$. $N=58$ *P. halepensis* plots, 16 *Q. ilex* plots and 15 mixed plots.

forest to *Q. ilex* forest and vice versa is similarly low. However, it should be taken into account that the study area has a relatively mesic climate, and probably these patterns could change in a more xeric area, where *P. halepensis* forms extensive forest stands (Quézel and Barbéro 1990) and is usually the only major forest tree (Quézel 2000). Moreover, the model does not incorporate temporal variability, because we have not information on survival of seedlings of the same age under different environmental conditions for establishing

the relationship weather/seedling survival and including temporal stochasticity in the model. This information (data of seedling survival in different post-fire meteorological conditions) is not available for this – and to our knowledge for any – species, probably because it requires an enormous sampling in different areas burned in different years.

The results obtained allow us to assess the role of heterogeneity before the fire in determining the changes produced in the forest types considered.

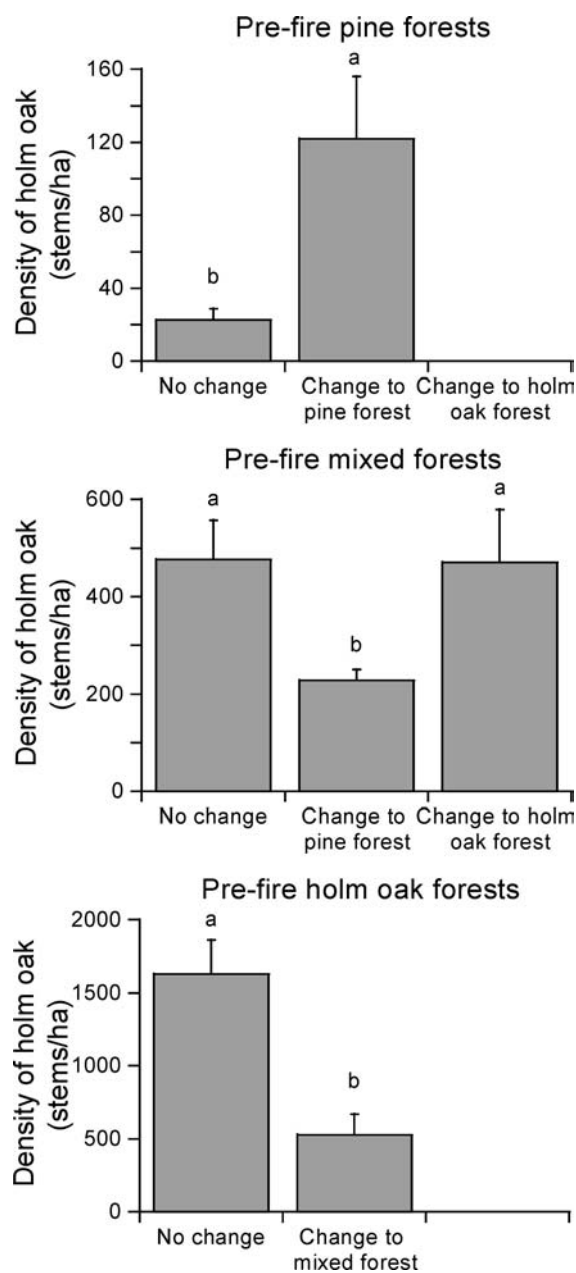


Figure 3. Density of holm oak trees (stems per ha) in plots of the three forest types (pine, mixed and holm oak forests) that remain the same forest type or change to another type 30 years after fire. Different letters indicate significantly different values at $p=0.05$ according to the Fisher's protected least significant difference *post-hoc* test.

Topographical variations were only significant for elevation. In the Mediterranean region, elevation is clearly related to the distribution of vegetation (Pigott and Pigott 1993). The effect of fire on the

distribution of the different forest types has been to increase the elevational differentiation between the two species because the *P. halepensis* forests that changed to mixed or *Q. ilex* forests were those of highest elevation, while the mixed and *Q. ilex* plots that changed to *P. halepensis* forests were those located at the lowest elevations. So, fire increases the gradient of species composition already described for the two species (Zavala et al. 2000), with *P. halepensis* proportion increasing towards the driest border and *Q. ilex* being the dominant species in areas with higher water availability.

The number of seedlings established after fire is more related to environmental conditions affecting them than to the number of seeds available (Barbéro et al. 1987; Herranz et al. 1997; Tsitsoni 1997). Thus, the density of *P. halepensis* trees before the fire only affects the probability of change of monospecific *P. halepensis* forests, but not that of the other forest types (Table 2). Concerning the density of *Q. ilex* trees before the fire, there is a high correlation between individuals before the fire and those resprouted after fire (Espelta et al. 1999). Density of *Q. ilex* individuals is variable in the rural areas because it goes up with time since abandonment as cropland (Broncano and Retana 2004). Thus, the widespread agricultural abandonment that has affected the countries of the northeastern Mediterranean basin (Vélez 1991; Puigdefábregas and Mendizábal 1998) has initially favored the expansion of *P. halepensis* in abandoned croplands and also of garrigue lands (Quézel 2000). However, this abandonment has been gradual, determining the density of *Q. ilex* individuals before the fire. Thus, the areas occupied by mixed forests correspond to old fields located at intermediate elevations that were abandoned long ago, and where *Q. ilex* was already established before the fire. On the other hand, the lower-elevation areas occupied at present by *P. halepensis* forests were those croplands abandoned more recently, where *Q. ilex* was not yet established.

Fire severity might affect the post-fire regeneration of forest communities (Whelan 1995; Turner et al. 1997, 1998). In the study area, patterns of burn severity affected the changes observed. For both *P. halepensis* and *Q. ilex* forests, plots that changed to another forest type were mostly those that burned with higher severity. This result agrees with the high resilience of monospecific forest of

these species, where changes only occur when disturbance is most severe. The high resistance of *P. halepensis* cones and, to a lesser extent, individual seeds to heat (Habrouk et al. 1999), means that it is only after very high temperatures that this species is not able to regenerate from seed sources in burned areas. In the case of *Q. ilex*, the effect of fire on the resprouting individuals is usually small (Espelta et al. 1999). Most individuals survive fire (Broncano and Retana 2004), mortality being usually restricted to small individuals at high fire severities. However, *Q. ilex* does not regenerate by seedlings in the post-fire scenario (Retana et al. 1999). In mixed forests, both species are expected to coexist if the disturbance regime allows the pines to capture openings earlier than *Q. ilex* ramets resprouted from individuals already present before fire (Zavala et al. 2000). In contrast, according to the results obtained in this study, as even low fire severities can produce high probabilities of change from mixed to monospecific forests, fire causes an increase in the segregation between the two species, especially because the high resilience of monospecific forests of these species can only be modified by very severe fire conditions or by frequent fires.

Acknowledgements

We are very grateful to Josep Maria Espelta and Xavier Picó for their very helpful comments on an earlier draft of the manuscript. This research was partly funded by INIA project SC98-070, and by EC project LUCIFER.

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