

Regeneration patterns of three Mediterranean pines and forest changes after a large wildfire in northeastern Spain

Introduction

Pines are important components in the vegetation of the Mediterranean Basin, where they cover more than 13 million ha at all elevations (Barbéro et al. 1998). According to Richardson & Rundel (1998), among the factors that have contributed to the rapid migration and population increases of different pine species are: abundant output of seeds from an early age, ability to recruit dense daughter stands on disturbed sites soon after disturbance, effective mechanisms for seed dispersal, and other traits that confer resilience at the population level under a wide range of disturbance regimes (i.e. wildfires). It is generally accepted that fire has favored pines throughout their natural range in the northern hemisphere, and even more in environments subject to chronic disturbances such as the Mediterranean Basin (Quézel 1980; Thanos & Marcou 1991; Agee 1998; Richardson & Rundel 1998). Pines have effectively exploited fire-prone environments by modifying their life cycle at different stages, from seed dispersal and seedling development, to adult tolerance and, to a lesser extent, vegetative regeneration (Keeley & Zedler 1998).

Pines dominate in many burned areas of the Mediterranean Basin (Trabaud 1987; Barbéro et al. 1998). This assumption mainly relies on studies carried out with *P. halepensis*, a fire-prone species that overcomes the destruction caused by fire through a very powerful mechanism of fire-induced seed release sufficient so as to regenerate the burned forest (Saracino et al. 1993; Daskalidou & Thanos 1996; Nathan & Ne'eman 2000). However, it misleads other pine species also abundant on the region, whose mechanism of fire recovery could be less effective. At present, this is particularly important if we take into account the change which has occurred in the fire regime in the last decades of the 20th century in the Mediterranean region, and which has led to a dramatic increase in fire frequency and extension (Moreno et al. 1998; Piñol et al. 1998). In the last few years, all types of Mediterranean pine forests have burned (Prieto 1995; Daskalidou & Thanos 1996; Arianoutsou & Ne'eman 2000). Larger and more intense wildfires are affecting both areas covered by fire-prone species, and areas with more mesic climatic conditions occupied by other *Pinus* species (Terradas 1996; Moreno et al. 1998).

Three of the most emblematic pine species of the Mediterranean Basin are abundant in the forested areas of the plains and middle elevations of the NE Iberian Peninsula: *Pinus halepensis* Mill., *P. nigra* (Arnold) and *P. sylvestris* L.. *P. halepensis* is a characteristic species from the semi-arid to sub-humid Mediterranean bioclimates (Quézel 2000), where it is generally abundant on the poorer soils and southern aspects (Kutiel & Naveh 1987). *P. nigra* is frequent in more humid and middle elevations, while *P. sylvestris* L. maintains large populations in middle and high elevated habitats of the north-west Mediterranean basin (Barbéro et al. 1998). Although the three species exhibit different preferences in their habitat, and thus, different geographical distribution patterns at the broad scale, there is a significant overlap in their distribution areas, with an important degree of coexistence at the local scale. In Catalonia (NE Spain), *P. nigra* coexists in more than 25% of its regional distribution area with *P. halepensis*, and in more than 35% with *P. sylvestris*. In the last seven years, large wildfires have severely affected 24.1% of *P. nigra*

plots, 12.1% of *P. halepensis* plots and 5.4% of *P. sylvestris* plots inventoried in the Forest Ecological Inventory of Catalonia (IEFC; Gracia et al. 2000).

In this study, the post-fire regeneration of these three pine species is analyzed in an area of central Catalonia (NE Spain) where the three pine species coexist, and which was affected by a large wildfire in summer 1994, when 24300 ha of forests dominated by these pine species were completely burned. The objectives of this study are: 1) to analyze the post-fire response of these three different pine species, and 2) to explore the effect of the differences in the regeneration success of these species on changes in their abundance and distribution in the frame of the present increment of fire size. The paper is based on two complementary approaches. First, we have assessed the regeneration pattern of *P. halepensis*, *P. nigra* and *P. sylvestris* by conducting a detailed sampling of tree regeneration in areas that were dominated by one of these pine species before the fire. Then, we have developed a model of succession to predict medium-term changes in forest composition 30 yr after fire from the regeneration monitored during the first three years after fire. We have predicted forest composition 30 years after fire using empirical information on the main demographic processes that occur in the post-fire regeneration of these species.

Material and methods

Study area

The study was carried out at the largest wildfire historically recorded in Catalonia (NE Spain). The fire occurred in July 1994, and burned ca. 24300 forested ha in the regions of Bages and Berguedà, located in central Catalonia (41° 45' to 42° 6' N; 1° 38' to 2° 1' E). The area was extensively covered by forests (71%), with some concentrated cropland areas (27%) and scarce shrublands and pastures (2%), and had not burned from at least 70 years ago. This large area had a wide range of climatic conditions, varying from dry-subhumid to subhumid Mediterranean (according to the Thornwaite index), with mean annual temperature of 10-13 °C and mean annual precipitation of 550-900 mm. The main tree species before the fire were three Pinus species (90% of the forested area), *P. nigra*, together with *P. halepensis* in the south of the burned area and with *P. sylvestris* in the north-east (Figure 1). There were also 10% of the forested area covered by two Quercus species (10% of the forested area), *Q. ilex* L. and *Q. cerrioides* Wk. et Costa. *Q. ilex* was more abundant than *Q. cerrioides* in *P. halepensis* forests (7% and 1%, respectively, of adult trees), while both species were similarly abundant in *P. nigra* (3% of adult trees) and *P. sylvestris* forests (4% of adult trees). Most trees, saplings and seedlings of all these species were completely burned after the fire, but many trees and large saplings of the two *Quercus* species resprouted vigorously after the fire. The three pine species considered were within their natural distribution range in Catalonia, and regenerate naturally in the absence of fire. The burned forests were located at altitudes ranging from 350 to 950 m above sea level, with a mean slope of 20°, and facing all aspects in a similar proportion (22% north, 24% east, 26% south and 28% west).

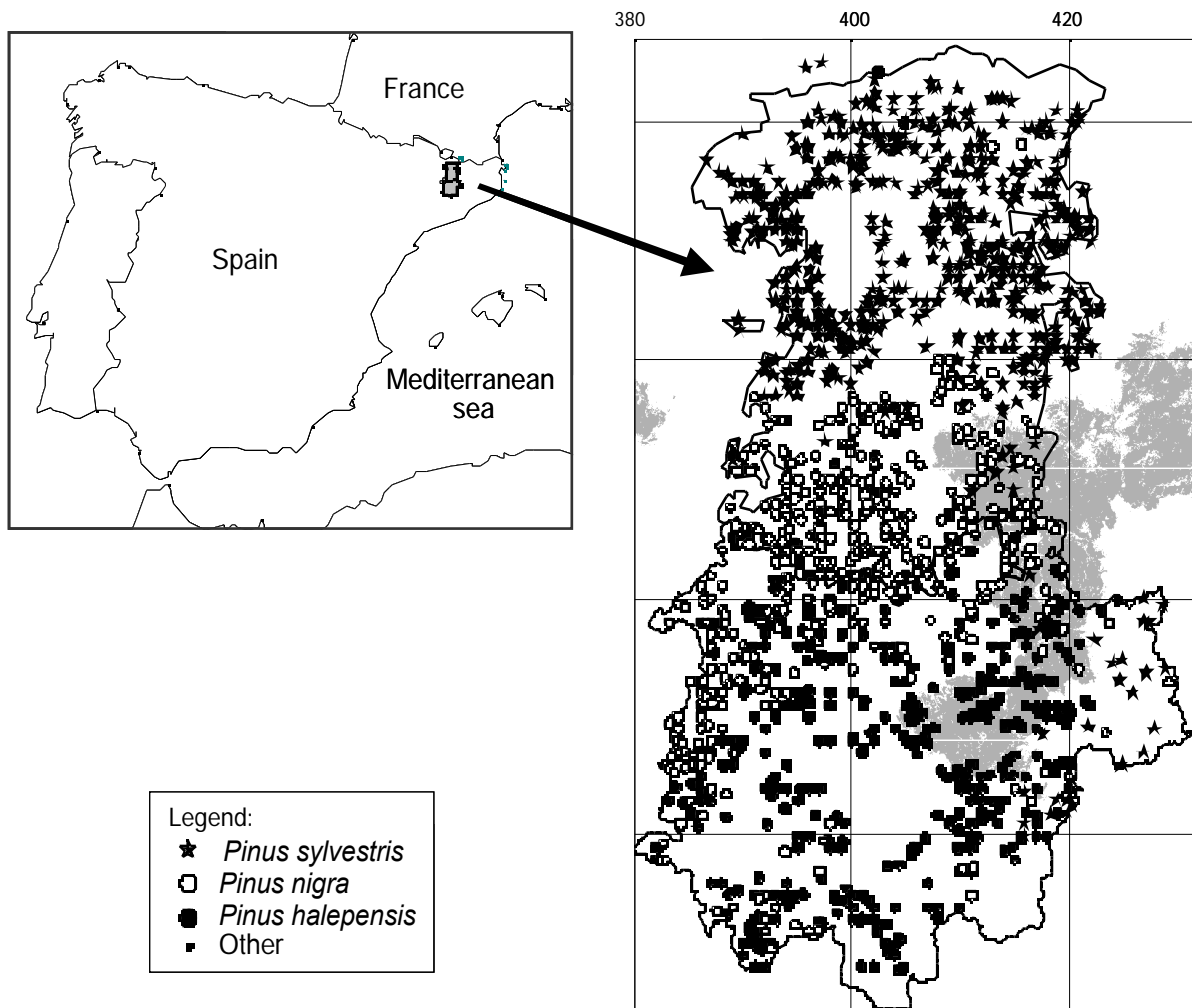


Figure 1. Geographical location of the regions of Bages and Berguedà, and distribution of plots from the Forest Ecological Inventory of Catalonia (IEFC), and the Second National Forest Inventory (IFN2) included in the area. The Universal Transverse Mercator (UTM) coordinates of the area are indicated. In grey, the whole surface burned in the fire of July 1994. Legend: black stars, plots dominated by *P. sylvestris*; open dots, plots dominated by *P. nigra*; solid dots, plots dominated by *P. halepensis*; small dots, other situations, which includes both plots dominated by other species and plots without dominance of any of the three pine species.

Sampling

The information used to analyze pre-fire forest composition and structure was obtained from the plots of the Forest Ecological Inventory of Catalonia (IEFC; Gracia et al. 2000), and the Second National Forest Inventory (IFN2; ICONA 1993) included in the whole burned area and sampled before the fire (in 1990-1993). The total number of plots used

was 329. In both inventories, sampling was carried out throughout the region at a plot density of one plot per km² of forested area. In each circular plot of 10-m radius, the following variables were determined: (a) topographical features: elevation, slope and aspect; (b) forest structure: density, basal area, mean dbh (diameter at breast height), and mean height of each tree species was determined by inventory of all stems in the plot with dbh larger than 5 cm. Wood production of each plot was also provided by the inventories' database, and estimated as the difference between the actual tree volume and the volume of the same tree 5 years earlier (Gracia et al. 2000). The main structural features of the forests of the three pine species are summarized in Table 1.

Due to the very large extension of the burned area, two different methods of post-fire data collection were carried out, an extensive sampling of the whole burned area, and a more-detailed sampling of a smaller number of plots:

- (1) *Extensive sampling.* An extensive survey of the entire burned area was carried out three years after the fire to assess the regeneration pattern of the main tree species present in the zone. Before the sampling, a precise determination of the burned area limits was conducted by comparing the Land Cover Map of Catalonia (Gracia et al., 2000) previous to the fire event, and aerial ortophotoimages 1:5000 taken 1 year after the fire (in summer 1995). The burned area was divided into homogeneous sampling areas based on the topography of the terrain, in order to facilitate and ameliorate the reliability of data collection. The surface of these sampling units ranged from 1 to 70 ha. The field survey of the regeneration included the monitoring of the percent of surface covered by the dominant tree species (*Pinus* and *Quercus*) in each sampling zone, through systematic visual observation (see Forman, 1995). The result of this survey was a map containing species cover in each sampling unit. We positioned all burned plots of the IEFC and the IFN2 considered (N=334) on this regeneration map, in order to determine the percent of surface covered by each species in each plot.
- (2) *Plot sampling.* A portion of the inventoried plots was exhaustively sampled three years after the fire. Only plots dominated by one of the three pine species (i.e., those that had more than 70% of stems of this species) were chosen: 44 *P. nigra* plots, 19 *P. halepensis* plots and 14 *P. sylvestris* plots. All plots were burned with crown fire, and did not contain living trees. Different measurements were carried out in each of these circular plots of 10-m radius. For sprouting *Quercus* species, the number of living trees was counted. New individuals of all tree species established after fire were counted in the whole plot. The number of pre-fire seedlings 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.

To assess natural regeneration in the absence of fire, fifteen control plots (i.e. not burned) dominated by each of the three pine species were also randomly chosen from all unburned plots of IEFC and IFN2 available in the same area. In these plots, all seedlings and saplings (i.e., individuals with dbh lower than 5 cm) of all tree species were counted and measured.

The effect of different climatic variables (data available from Ninyerola, Pons & Roure in press), such as total rainfall, spring rainfall, autumn rainfall, mean temperature, mean summer maximum temperature and mean winter minimum temperature, was not tested since previous analyses showed that they were highly correlated with elevation ($r > 0.85$ in all cases).

Table 1. Main forest structural features before the fire. This information was obtained from the forest plots of the Forest Ecological Inventory of Catalonia (IEFC) and the Second National Forest Inventory (IFN2) inventoried in the whole burned area before the fire. N, number of plots. Data are shown as mean \pm standard error.

Forest type	N	Elevation (m)	% Pines in the canopy	Density (stems/ha)	Basal area (m ² /ha)	Dominant height (m)
<i>P. halepensis</i>	62	250-700	91 \pm 10	865 \pm 366	11 \pm 6	10 \pm 4
<i>P. nigra</i>	241	350-850	90 \pm 9	1139 \pm 301	18 \pm 8	13 \pm 4
<i>P. sylvestris</i>	31	500-950	85 \pm 10	1054 \pm 292	18 \pm 7	15 \pm 4

Statistics

Statistical differences of the different topographic (except aspect) and pre-fire structural variables of burned plots that change to different forest types after the fire were analyzed using one-way ANOVAs, with post-fire forest type as fixed factor. Then, the individual mean values of the three post-fire forest types were compared with a post-hoc test (Fisher's protected least significant difference). In all cases, inspection of residuals was carried out to check for normality and homoscedasticity. When necessary, analyses were run on log transformed data. To compare the number of plots from the different slopes (north, east, south and west, each category of 90°) that changed to the different forest types after the fire, different χ^2 tests were carried out for plots dominated by one of the three pine species before the fire.

The model

The post-fire forest type of each plot was defined as the potential vegetation 30 years after the fire. This time was chosen because, in these Mediterranean forests, it is the period of time elapsed to close the canopy (Espelta et al. 1995) and the burned area recovers the appearance of forest (Trabaud 1991). The future vegetation in each plot was predicted from the tree regeneration data recorded in each plot in the field. As densities of individuals of the different tree species were the main parameters used to predict future forest composition, we needed this information for all the 329 plots used. However, we only had density values for the 85 plots included in the plot sampling, and not for the remainder considered only in the extensive survey. For this reason, we transformed the cover percentages obtained in the extensive field survey to density values. We thus computed the linear regression between cover data obtained in the extensive sampling and seedling density obtained in the plot sampling using the data from the plots included in both samplings. From the equations 1 and 2 (Table 2), we computed density values of *P. halepensis* and *Quercus* spp. in all plots included in the extensive sampling.

The projection of density values of the different species just after fire to 30 years later was carried out as:

- The number of *P. halepensis* individuals 30 years after fire was estimated as the number of the initial seedlings in the plot that survived 30 years later. This value was obtained as the product of the initial number of seedlings and the proportion of seedlings surviving 30 years after fire. According to equation 3 (Table 2), 41.1% of *P. halepensis* seedlings survive 30 years after fire. Postfire regeneration of the other *Pinus* species was very low (see Results) and, since survival data for them were not available, the seedling survival curve of *P. halepensis* was also used for these species. According to different authors (Daskalakou & Thanos 1996; Herranz et al. 1997; Thanos 1999; Broncano 2000), we assumed that the incorporation of new recruits after the first regeneration flush was negligible or nil.
- Total stem density of the different resprouter oak species 30 years after fire was calculated as individual (=genet) density times expected number of stems per stool after 30 years. Individual density was obtained directly from the plots, while the number of stems per stool 30 years after disturbance was 3.6 for *Q. ilex* (determined from equation 4 in Table 2), and 1.9 for *Q. cerrroides* (determined from equation 5 in Table 2, obtained by the authors by fitting the data of the number of stems per individual of *Q. cerrroides* measured in 4 stands at different times from the last fire -3, 11, 17 and 24 years-). We assumed that mortality of resprouter individuals surviving fire was nil during the period of 30 years after fire (Espelta, Sabaté and Retana, 1999).

Three different types of plots were defined according to these estimated values of the composition (in number of stems) of the vegetation of each plot 30 years after the fire:

- Shrubland plots were defined as those with less than 10% of tree cover, following the criterion used in the IEFC (Gracia et al. 2000). For each plot, cover data were estimated from tree density values by computing the regression equations between cover and density for each species using data from the IEFC. When there were two or more species in the plot, the weighted cover value according to the proportion of each species in the plot was used.
- *P. halepensis* plots, either monospecific or mixed with *Quercus* species, were defined as those forest plots with a density of *P. halepensis* higher than 33.3% of total tree density.
- Oak-dominated plots were defined as those forest plots with a density of *Quercus* spp. higher than 33.3% of total tree density (except those with a density of *P. halepensis* higher than 33.3%, which were included in the former type).

Table 2. Equations used to describe the different processes considered in the model of vegetation dynamics. Ph, *Pinus halepensis*.

Equation	Formula	y	x	a	b	R ²	p	Reference
1	y=bx+a	Ph density	Ph cover	-5128	2294	0.53	<0.001	IEFC
2	y=bx+a	oak density	oak cover	-258	45	0.45	<0.001	IEFC
3	y=ax ^b	Ph survival	time after fire	104.5	-0.274	0.86	<0.001	Broncano 2000
4	y=a10 ^b x	stems/stool	time after disturbance	143.8	-0.053	0.98	<0.01	Retana et al. 1992
5	y=a+b log x	stems/stool	time after fire	11.8	-6.7	0.93	0.019	this study

To determine changes in forest composition after fire for each pine species, the probability of remaining as the same forest type or changing to another type were determined as the percent of plots that were categorized after the fire in each of these three post-fire types.

Results

Pre-and post-fire regeneration patterns

In the absence of fire, regeneration of tree species in forests dominated by each of the three pine species was considerable (Table 3). Regeneration of each pine species was high in forests dominated by the same species. However, it was much lower or nil in plots dominated by the other pines. Density of *Quercus* (*Q. ilex* and *Q. cerrrioides*) regeneration was very high in the three forest types, especially in plots dominated by *P. sylvestris*.

Regeneration of tree species in burned plots was completely different (Table 4). *P. halepensis* showed very high post-fire seedling densities in *P. halepensis* plots. This species showed low densities in plots dominated by *P. nigra* before the fire, but it should be taken into account that only in one of the 44 *P.nigra* plots sampled there were some *P.*

halepensis trees in the canopy before the fire. *P. nigra* and *P. sylvestris* almost disappeared from burned plots, because seedling densities were almost nil in the three forest types. Density of *Q. ilex* and *Q. cerrrioides* was considerably reduced in burned plots, due to the high mortality of seedlings and small saplings present before the fire, but there was still a percent of juveniles that sprouted vigorously after fire. No new *Quercus* individuals were registered in the burned plots.

Changes in tree sominance after fire

Based on the post-fire regeneration values of the different tree species, the probability of each pre-fire forest type remaining as the same forest type or changing to another type was determined for the forests of the three pine species. The patterns of change strongly depended on the dominant pine species present before the fire (Figure 2). In the case of *P. halepensis* forests, nearly 75% of burned plots showed enough regeneration of *P. halepensis* to warrant the existence of monospecific or mixed forests of this species after the fire. On the contrary, none of the plots dominated by *P. nigra* or *P. sylvestris* remained as the same forest type after the fire. Moreover, 7% of plots dominated by *P. nigra* before the fire showed a large post-fire regeneration of *P. halepensis* originated from seeds produced by the rare *P. halepensis* trees present in the canopy before the fire.

Except this percent of *P. nigra* plots which changed into *P. halepensis* plots, the remaining plots that changed after the fire were transformed into two forest types (Figure 2). The majority of plots changed to a forest dominated by *Q. ilex* and *Q. cerrrioides* resprouted after the fire which would develop into future monospecific or mixed oak forests. This proportion of burned plots dominated by oaks after the fire increased from *P. halepensis* forests to *P. nigra* and *P. sylvestris* ones. In the remaining cases, the original forest was replaced by open shrublands with very low density of tree species. The proportion of plots changing to shrubland after fire was highest in *P. nigra* forests (16.3%) and decreased in *P. sylvestris* (7.1%) and *P. halepensis* forests (5.3%, although it represents in this case 21.2% of plots that changed to another forest type).

Table 3. Number (mean±standard error) of seedlings and saplings of the different tree species regenerated per ha in unburned forests dominated by each of the three pines considered. N=15 plots for each forest type.

	<i>P. halepensis</i>	<i>P. nigra</i>	<i>P. sylvestris</i>	<i>Q. ilex</i>	<i>Q. cerrrioides</i>
Forest type regeneration	regeneration	regeneration	regeneration	regeneration	regeneration
<i>P. halepensis</i>	1904±349	16±9	0	2180±1060	681±390
<i>P. nigra</i>	182±141	1612±426	107±28	2418±778	792±370
<i>P. sylvestris</i>	0	22±15	1407±492	2384±1300	2386±659

Table 4. Number (mean±standard error) of seedlings and saplings of the different tree species regenerated per ha in burned forests dominated by each of the three pines considered. N=19, 44 and 14 *P. halepensis*, *P. nigra* and *P. sylvestris* plots, respectively. The regeneration of the two *Quercus* species includes pre-fire seedlings and saplings that were burned but sprouted after fire. No new *Quercus* individuals were registered in the burned plots.

	<i>P. halepensis</i>	<i>P. nigra</i>	<i>P. sylvestris</i>	<i>Q. ilex</i>	<i>Q. cerrioides</i>
Forest type regeneration	regeneration	regeneration	regeneration	regeneration	regeneration
<i>P. halepensis</i>	12350±5272	1±1	0	186±87	136±68
<i>P. nigra</i>	69±27	7±3	1±1	163±36	164±36
<i>P. sylvestris</i>	1±1	0	18±13	186±72	773±286

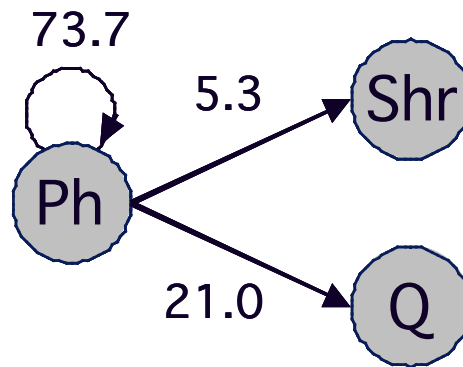
Environmental and pre-fire structural features determining post-fire changes

Table 5 shows the comparison of topographic and structural variables before the fire of the plots of the three pine species that changed to different forest types after the fire. *P. halepensis* plots that changed to oak-dominated woodlands were predominantly located in the highest elevations of the distribution of this species before the fire. These plots changing to oak woodlands were also those with the highest pine density, basal area and dbh before the fire.

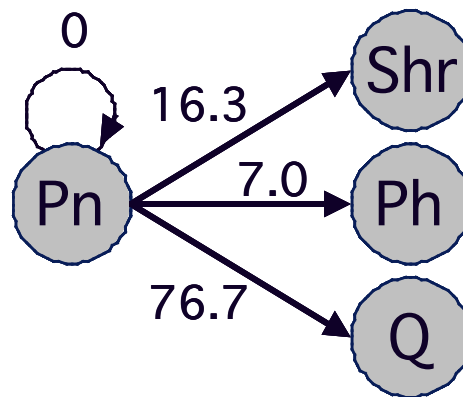
Elevation was the only variable that showed significant differences among *P. nigra* plots changing to different forest types after fire: plots placed at the lowest elevations and close to *P. halepensis* forests changed mainly to plots dominated by *P. halepensis*, while there were no differences in elevation between plots changing to shrublands or to oak-dominated communities (Table 5). None of the variables considered showed significant differences between *P. sylvestris* plots changing to shrubland and those changing to oak forest. Pine production and mean pine height did not show significant differences among post-fire destination communities for any of the three pine species.

There were no significant differences in the number of plots from the different slopes (north, east, south and west) that changed to the different forest types after the fire for any of the three pine species considered (χ^2 test, $p > 0.50$ in all cases).

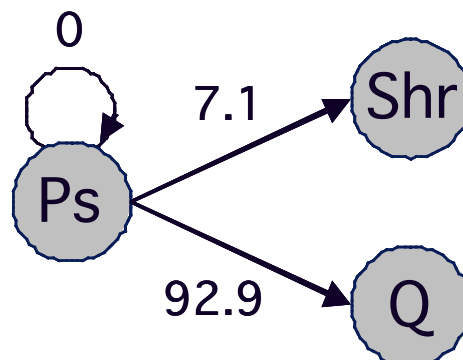
Pinus halepensis



Pinus nigra



Pinus sylvestris



Bm Figure 2. Probability of the forests of the three pine species remaining as the same pre-fire forest type or changing to another type 30 years after fire. Legend: Shr, shrubland; Ph, *P. halepensis* forest; Q, oak forest (either of *Q. ilex*, *Q. cerrrioides* or both). N=61, 237 and 31 pre-fire *P. halepensis*, *P. nigra* and *P. sylvestris* plots, respectively.

Table 5. Comparison of topographic and structural variables before fire of burned plots that change to different forest types after fire (Shru, shrubland; Phal, forest of *Pinus halepensis*; Oak, oak-dominated forest). Forests dominated by each of the three pine species are considered separately. F values and statistical significance of the ANOVAs carried out for the different variables are shown, together with the mean value for each post-fire forest type. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; NS, not significant. Significantly different means, based on Fisher LSD F-test (at $p = 0.05$), are indicated by different letters. $N = 62$, 241 and 31 pre-fire *P. halepensis*, *P. nigra* and *P. sylvestris* plots, respectively.

Variable	<i>P. halepensis</i>				<i>P. nigra</i>				<i>P. sylvestris</i>		
	F	Shru	Phal	Oak	F	Shru	Phal	Oak	F	Shru	Oak
Elevation (m)	5.0 **	511 a	509 a	678 b	14.0 ***	595 b	518 a	612 b	NS	761	668
Slope (°)	NS	19	21	20	NS	16	19	17	NS	20	20
Pine density (pines ha ⁻¹)	3.8 *	526 a	849 ab	903 b	NS	1112	1114	1111	NS	975	1153
Pine basal area (m ² ha ⁻¹)	4.5 *	8.7 a	9.4 a	16.8 b	NS	17.6	18.2	18.0	NS	17.2	17.2
Pine production (m ³ ha ⁻¹ yr ⁻¹)	NS	1.3	1.3	1.6	NS	2.7	2.9	2.8	NS	2.8	3.5
Mean pine dbh (cm)	7.2 **	12.0 a	16.0 b	16.2 b	NS	15.0	15.4	14.9	NS	15.9	14.3
Mean pine height (m)	NS	10.0	9.6	10.9	NS	13.0	13.9	13.7	NS	14.7	13.4

Discussion

Pre-and post-fire regeneration patterns

The results obtained in this study show that the post-fire regeneration of three pine species is very different (Table 4), although they regenerate quite well in the absence of fire in forests where they dominate the canopy (Table 3). *P. halepensis* shows a high but irregular regeneration that allows the recovery of burned forests after fire, but *P. nigra* and *P. sylvestris* almost disappear from burned plots, because their seedling densities are almost nil. Several reproductive traits of these species may explain these important differences. First, *P. halepensis* is a serotinous tree, which disperses only a part of its canopy-stored seeds, and safeguards the rest in a long-term canopy seed bank (Nathan & Ne'eman 2000). The seeds are released from cones only by the heat and the dryness induced by a severe wildfire (Saracino et al. 1993; Daskalidou & Thanos 1996) or by a dry and hot drought event in the absence of fire (Nathan et al. 1999). A massive wave of seed germination occurs immediately after the onset of the rainy season (Thanos 1999), creating an almost even-aged wave of pine regeneration (Ne'eman & Izhaki 1998), because few or no additional seedlings are usually observed after the first post-fire year (Herranz et al. 1997; Thanos 1999; Broncano 2000).

Second, *P. halepensis* seedlings are highly tolerant to hydric stress (Espelta, 1996; Zavala, Espelta & Retana 2000), which allows them to resist the harsh environmental conditions that they find in burned areas, with high temperatures and a bare soil favoring water losses. On the other hand, *P. nigra* and *P. sylvestris* do not have serotinous cones (Lanner 1998). They show a similar seeding phenology, with dispersal of seeds occurring in late winter to early spring (Bolos & Vigo 1984; Laguna 1993; Skordilis & Thanos 1997). Then, in summer, that is the period of most fires in the Mediterranean region (Peix 1999), most cones are empty and the seed canopy bank is exhausted. The only viable source of seeds for regeneration after summer fire is thus the soil seed bank. However, pine soil seed banks are transient (Trabaud et al. 1997; Izhaki & Ne'eman 1998; Broncano 2000). In the case of *P. nigra* and *P. sylvestris*, most seeds have already germinated in spring (pers. obs.), and fire consequently burned the seedlings. The few seeds that remain in the soil are not able to resist the high temperatures attained during intense summer wildfires (Habrouk et al. 1999).

After the passage of fire, the only new source of *P. nigra* or *P. sylvestris* seeds in the burned areas is the arrival of propagules from the unburned margins. However, the distance at which pine seeds are dispersed is usually short, less than ca. 50 m, both for *P. halepensis* (Acherar et al. 1984; Papió 1990; Broncano 2000; Nathan et al. 2000) and *P. nigra* (Ordóñez, unpublished data). Under this constraint, the size of disturbed patches influences propagule availability and, thus, vegetation composition (Kneeshaw & Bergeron 1998; Turner et al., 1998). In large burned patches (>500 ha), the proportion of total surface with high seedling density is extremely low, and colonization from the surrounding unburned landscape is likely to take many decades. In contrast, densities of tree seedlings in small patches (1-2 ha) of similar burn severity

are considerably higher because of greater seed input from nearby unburned areas throughout the whole burned area. This pattern has been confirmed for *P. nigra*, which can be re-established few years after the fire in small burned areas from seeds coming from the unburned margin (Toth 1987; Roig 1997), but that almost disappears from burned plots in a large fire (like in this case). So, the potential to colonize burned areas exists for these pine species, it is the area of fires which ultimately may change pine distribution.

Changes in tree dominance due to fire

Fire is considered the main disturbance factor that occurs with sufficient frequency and intensity to be a consistent and strong selective pressure affecting the radiation and distribution of tree species (Keeley & Zedler 1998). In Mediterranean landscapes, the theory suggests that there is no real succession after fire in the sense of replacement of species or communities, but only a progressive return towards a stage similar to that existing before the fire (Hanes, 1971; Zedler et al. 1983; Keeley 1986; Arianoutsou 1998; Trabaud 2000). This is probably true for communities where the majority of studies on post-fire regeneration have been carried out, such as shrublands or pine forests of *P. halepensis* or *P. brutia*, which are affected by high fire frequencies (between 5 and 50 years). The permanence in the canopy of these pine species depends, to a certain extent, on fire: in the absence of fire for 100 years or more, these species might disappear locally from the landscape (Naveh 1990), although this is a remote possibility given the current fire patterns (Agee 1998). Moreover, although several authors (Trabaud et al. 1993; Agee 1998) suggest that *P. halepensis* may expand its range after fire into areas previously occupied by forests of the less fire-tolerant pines, only in the lower-elevation *P. nigra* stands (those which are probably in the proximity of the source of propagules of *P. halepensis*), this species was replaced in the forest canopy by *P. halepensis* (Figure 2, and Table 5).

It has been suggested that few if any species of the genus *Pinus* have no adaptations to fire (Agee 1998). However, the potential recovery of pine populations after fire does not match the results obtained in the present study for forests dominated by *P. nigra* and *P. sylvestris*. These two species depend only on seed dispersal from nearby seed bearers for recovery after fire, at least in the short- and medium-term. When the forests of these species burn, there are major changes that affect both the structure and the composition of the post-fire vegetation. For this reason, the present fire regime may represent a major factor affecting, on a short time scale, the dynamics of monospecific or mixed forests dominated by these pine species and, on a longer time scale, their geographical distribution. The highest proportion of plots originally dominated by pines changes after fire to communities dominated by oaks (*Q. ilex*, *Q. cerrrioides*). Although a high proportion of the pre-fire oak seedlings and saplings present in the understory of the *Pinus* stands die after the passage of fire (Tables 3 and 4), there is still a considerable percent which sprouts vigorously and allows oak dominance in the future forest. In general, the replacement pine-oak is in accordance with the patterns of vegetation dynamics described for the Mediterranean Basin (Quèzel & Barbéro 1987; Barbéro et al. 1998): *P. halepensis* is mainly replaced by *Q. ilex*, but also by *Q. cerrrioides*; *P. nigra* is replaced either by *Q. ilex* or *Q. cerrrioides*, while *P. sylvestris* is

almost always replaced by deciduous oaks (i.e. *Q. cerrioides*).

There is also a considerable percent of burned pine plots that changes to shrublands. In plots dominated by *P. halepensis* before the fire, they represent one third of plots that change to another forest type. Compared to plots dominated by oaks after the fire, shrubland plots correspond to the areas with lower elevation and lower annual rainfall, and also those which had less-structured *P. halepensis* forests (see Table 5). These areas were probably abandoned as croplands a few years previously and, thus, had fewer oaks established in the understory. In fact, different evidences from this previous agricultural use in recent years can be observed in situ. The percent of plots that changes to shrublands increases for the other two pines, especially in the case of stands dominated by *P. nigra* before the fire (Figure 2). However, the lack of statistical differences in topographic and pre-fire forest structural variables for these two pine species suggest that changes in forest composition after fire (either to shrubland or to oak woodland) only depend on the presence of a source of acorn production in the nearby area, that allows the establishment of oaks before the fire. Overall, and according to the simulations used in this study, throughout the burned area there is an increase in the percent of surface covered by shrublands from less than 2% before the fire to roughly 29% 30 years after the fire. This important increase in shrubland areas has to be considered with caution, because the high cover and horizontal continuity of these shrubland areas could increase the risk of more frequent and recursive wildfires in the future (Vélez 2000).

The present results suggests a large scale change in the woody vegetation dynamics promoted by large fires in the area of study, because of (i) the lack of efficient regeneration mechanism in some of the pine species involved, and (ii) the difficulties to colonise the burn area from the distant borders. However, vegetation changes promoted by the large fire, i.e. conversion of pine forests to oak woodlands or shrublands, seems to be related with the previous history of land-use pattern. This area, as well as similar Mediterranean areas in France and Italy, have experienced major land-use changes during the 20th century that have led to the progressive abandonment of marginal agricultural lands thus triggering an expansion and spread of pine forests (Di Castri 1998). The transformation of pine forests into shrublands or oak woodlands seems related with the time lag from abandonment, with the more recently abandoned lands becoming shrublands, while the older areas, those providing time and a suitable habitat for oaks to establish (see, Lookingbill & Zavala 2000), turning after the fire into oak woodlands.

Conclusions

The extrapolation of the changes predicted by the simulations in the inventoried plots to the whole burned area points to important consequences on the overall distribution of the three pine species considered. The smallest variations are expected to occur in *P. halepensis* forests, but even in this case the percent of plots where *P. halepensis* is present decreases from 33.7% before the fire to 24.9% in the burned area. This raises some doubts concerning the traditionally-considered high resilience of this species (Thanos 1999; Trabaud 2000). The consequences of

the fire event for the other two species are much more dramatic. *P. nigra* was the dominant species in the area before the fire, but almost disappears after the fire (Figure 2). Since *P. nigra* has become in the last few years one of the tree species that has suffered the greatest fire destruction in Catalonia, this lack of post-fire recovery might have serious consequences on its distribution range in the region (de Bolós & Vigo 1984; Barbero et al. 1998). The third pine species considered, *P. sylvestris*, was dominant, either alone or mixed with other species, in 14.4% of the inventory plots in the Bages-Berguedà area before the fire, but that was absent from burned plots. In this case, fire might also have dramatic consequences for the populations of this species. *P. sylvestris*, which is characteristic of boreal and temperate forests of central and northern Europe, and only has relict populations throughout the northern Mediterranean Basin (Barbero et al., 1998; Richardson & Rundel 1998). The inability of *P. nigra* and *P. sylvestris* to recover after fire indicates that there are species living in the Mediterranean area that might be strongly affected by wildfires. However, the knowledge about the response of plant species after fire is only available for a small array of Mediterranean species. More studies are needed because, in the present fire scenario, which is characterized by an increase in the number and size of wildfires (Moreno et al. 1998; Piñol et al. 1998), information about the effect of repeated fires of different intensities and sizes on vegetation is basic to our understanding of changes in the abundance and distribution of species.

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