Forest Ecology and Management

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

History matters: Previous land use changes determine post-fire vegetation recovery in forested Mediterranean landscapes

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ARTICLE INFO

ABSTRACT

Land use changes and shifts in disturbance regimes (e.g. wildfires) are recognized worldwide as two of the major drivers of the current global change in terrestrial ecosystems. We expect that, in areas with large-scale land use changes, legacies from previous land uses persist and affect current ecosystem responses to climate-associated disturbances like fire. This study analyses whether post-fire vegetation dynamics may differ according to specific historical land use histories in a Mediterranean forest landscape of about 60,000 ha that was burnt by extensive fires. For that, we assessed land use history of the whole area through the second half of the XXth century, and evaluated the post-fire regeneration success in terms of: (i) forest cover and (ii) tree species composition (biotic-dispersed, resprouter species, Quercus spp. vs. wind-dispersed species with or without fire-resistant seed bank, Pinus spp.). Results showed that stable forest areas exhibited a higher post-fire recovery than younger forests. Furthermore, the longer since crop abandonment translates into a faster post-fire recovery. Results highlight that to anticipate the impacts of disturbances on ecosystems, historical land trajectories should be taken into account.

1. Introduction

Understanding the interactions between different drivers of global change is one of the key present challenges among politicians, economists, ecologists, and society in general (IPCC, 2007; FAO et al., 2008). Land use changes and shifts in disturbance regimes (e.g. wildfires) are recognized worldwide as two of the major drivers of the current global change in terrestrial ecosystems (Vitousek, 1992; Rudel et al., 2005; Fraterrigo et al., 2006; Hermy and Verheyen, 2007). Surprisingly, the interaction between past land uses and fire impacts has received little attention. However, their tight coexistence can make us hypothesize that fire may have different effects in areas undergoing different land use trajectories in the past (Duguy et al., 2007; Walck et al., 2011). The Mediterranean rim may act as an ideal scenario to analyze the interaction between disturbances, such as fire, and land use changes (in particular crop abandonment) because both components of global change are largely present in many areas since the last decades (Blondel and Aronson, 1999; Palahí et al., 2008). In the northern rim of the Mediterranean Basin, the general trend to the abandonment of less fertile agricultural areas during the second half of the XXth century has resulted in an increasing expansion and connectivity of woodlands, particularly by either natural colonization and densification of the existing forests or, to a lesser extent, by active afforestation (Debussche et al., 1996; Lloret et al., 2002; Mouillot et al., 2005; Améztegui et al., 2010). Vegetation recovery has been argued in turn to be a major factor behind recent changes in fire regime together with changing climate conditions leading to an increase number of fire prone days per year (Piñol et al., 1998; Rudel et al., 2005). Indeed, the increase in fire recurrence and surface burned in the recent decades in Mediterranean-type forests and shrublands has been attributed to extensive forest recovery (Pausas, 2004).

Plant responses to fire and cropland abandonment are likely to be determined by species-specific functional traits (Pausas, 1999; Mouillot et al., 2005). In the present global change context, advancing in the understanding of these mechanisms is critical since they may play a determinant role for the maintenance (e.g. reduce soil erosion) and functioning (e.g. carbon sequestration) of forest ecosystems (Rudel et al., 2005; Thompson et al., 2009; FAO et al.,

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2008). Land use changes are known to impact different ecological processes and influence soil properties (Fraterrigo et al., 2006; Hermy and Verheyen, 2007) leading to the general hypothesis that areas undergoing different land use trajectories are likely to differently respond to fire thus leading to differences in post-fire regeneration patterns (Duguy et al., 2007; Walck et al., 2011; Foster, 1992).

Specific land use changes over time are likely to leave a strong signal on the capacity of the system to respond to fire. Land use changes might modulate the relative presence of species having distinct functional traits (Foster, 1992; Hermy and Verheyen, 2007) which can be related to post-fire responses (Pausas et al., 1999; Rodrigo et al., 2004). For example, small-seeded, wind-dispersed woody species (e.g. *Pinus* sp) are generally early pioneers that successfully quickly colonize abandoned croplands (Richardson and Rejmánek, 2004; Picon-Cochard et al., 2006). Since these species do not resprout after fire, post-fire regeneration will be totally dependent on seed dispersal from nearby unburnt adults or a viable seed bank after fire (Rodrigo et al., 2004). On the other hand, large-seed and biotic-dispersed species (e.g. *Quercus* sp) will be short-distance passively dispersed and will require some degree of previous perches and vegetation shelter to ensure effective biotic dispersal and further establishment (Gómez et al., 2008; Gómez-Aparicio et al., 2009; García et al., 2010; Zamora et al., 2010), which implies a slower colonization rate in open areas (such as crops recently abandoned). However, once established, these species will be highly resilient to fire occurrence, as post-fire natural regeneration is usually guaranteed by resprouting from protected buds, thus maintaining the same individuaĺs density in the burnt area (López-Soria and Castell, 1992; Espelta et al., 2003; Bonfil et al., 2004).

The main objective of this study is to analyze whether post-fire vegetation regeneration differ according to specific historical land use trajectories. We hypothesized that time since land abandonment will determine pre-fire vegetation (abundance of resprouters in the case of *Quercus* sp. and *Pinus* sp. with or without fire-resistant canopy seed bank based on serotinous cones, hereafter resprouters and serotinous/nonserotinous species) and thus be a critical factor determining post-fire regeneration. This hypothesis was tested in an area burnt by two extensive wildfires (c.a. 60,000 ha). We analyzed the relationship between land use history (years 1956, 1978 and 1993) and the post-fire regeneration success in terms of land cover and species composition (biotic-dispersed and resprouter species, *Quercus* spp. vs. wind-dispersed serotinous or nonserotinous species, *Pinus* spp.). According to the functional traits of these species, we expected that: (i) changes in forest cover after fire will depend on land use trajectory of the site, i.e. long standing forest areas will exhibit a higher and faster recovery that those that recently became forested, ii) species composition will depend on previous land uses and fire history: presence of *Quercus* sp. (resprouters) in the site will be influenced by time since cropland abandonment and not by fire occurrence while the presence of *Pinus* sp (seeders) will be less conditioned by time since cropland abandonment and more determined by fire and iii) whatever the influence of land use history in post-fire recovery, this process will vary along the landscape, being faster in northern aspect sites (i.e. cooler and more humid) than in southern sites, due to the general and critical water deficit that characterizes the Mediterranean climate.

2. Materials and methods

2.1. Species and study area

The study area comprises 63.190 ha distributed in Catalonia (NE Spain, 41°45′–42°6′N; 1°38′-2°1′E Fig. 1). The area presents a gentle relief with low hills ranging in elevation 320–1500 m.a.s.l. and a dry-sub-humid to sub-humid Mediterranean climate (according to the Thornwaite index), with mean annual temperature 10–13 °C and annual precipitation ranging 600–900 mm. According to the data provided by the Forest Ecological Inventory of Catalonia (IEFC; Gracia et al., 2002) and the Spanish Second National Forest Inventory (NFI2; ICONA, 1993–2000), in 1990 the area was extensively covered by a mosaic landscape of forests (71%), cereal croplands (27%) and scarce shrublands and pastures (2%). The dominant forest tree species in the area were: *Pinus nigra* Arnold (63% of the forested area), *Pinus halepensis* Mill. (18%), *Pinus sylvestris* L. (14%) and mixed *Quercus ilex* L. and *Quercus cerrioides* Wk. *et* Costa forests (5%). While none of the *Pinus* species can resprout and all have small wind-dispersed seeds, only *P. halepensis* possesses a fire-resistant canopy seed bank which can release their seeds after fire (Habrouk et al., 1999; Tapias et al., 2004). On the contrary, *Quercus* species can resprout and have bigger seeds biotically dispersed mainly by jays and rodents (Gómez, 2003; Gómez et al., 2008).

In 1994 and 1998, two extensive summer wildfires burnt 61% of the surface included in the study area (c.a 24.300 ha in 1994 and 14.300 ha in 1998). These extremely intense crown fires, resulted in the lost of almost all above-ground living biomass of trees inside the perimeter of the burnt surface (Retana et al., 2002). Before these fire events, the area had not burned for at least 70 years (Espelta et al., 2002).

2.2. Land use histories and estimation of forest responses to fire

We used two complimentary data sources to gather information on spatial heterogeneity in post-fire vegetation responses: (1) forest inventory data, based on permanents plots to gather species-specific information and (2) remote sensing imagery, based on a wider area to obtain estimates of forest densification.

First, we used 565 plots (25 m radius) covering the study area using a 1×1 km systematic sampling carried out in 1993 (before the fire events) during the Spanish Second National Forest Inventory (NFI2; ICONA, 1993–2000) and re-sampled again in 2001 during the Spanish Third National Forest Inventory (NFI3; DGCN, 2005). In the study area NFI plots are set in areas with no post-fire management of forests.

Comparison of the data provided by the NFI2 and the NFI3 allowed us to identify whether a given plot had burnt during the 1994 and 1998 wildfires (249 plots burned out of 565, 44%). Presence and density (stems/ha) of the five tree forest species dominant in the area (*Q. ilex* and *Q. cerrioides* (resprouters with biotic-dispersed seeds); *P. nigra, P. sylvestris* (non-serotinous and wind-dispersed seed) and *P. halepensis* (serotinous and wind-dispersed seeds) was assessed in the 565 plots through the NFI3 forest inventory dataset carried out in 2001. The density of each species includes stems >2.5 cm of basal diameter. To account for the presence of each species, apart of stems >2.5 cm, we also considered the presence (or absence) of individuals <2.5 cm diameter.

Since 1993 all plots were considered to be within a forested land use category as they had been included in both the second and third national forest inventories (NFI2, NFI3). Previous land use in the inventoried plots (forests, *F*, or croplands, *C*) was assessed from (1) direct photointerpretation of aerial photographs (year 1956) and (2) the existing land use map of the Spanish Ministerio de Agricultura, Pesca y Alimentación (Mapa de Cultivos y Aprovechamientos) (year 1978). This allowed us to assign to each plot of the NFI a historical land use trajectory: CCF (cropland in 1956 and 1978, forest in 1993), CFF (cropland in 1956, forest in 1978 and 1993) and FFF (forest in 1956, 1978 and 1993) (see Fig. 1). Plots in the category FCF (forest in 1956, cropland in 1978, and forest in 1993) were excluded because of their low num-
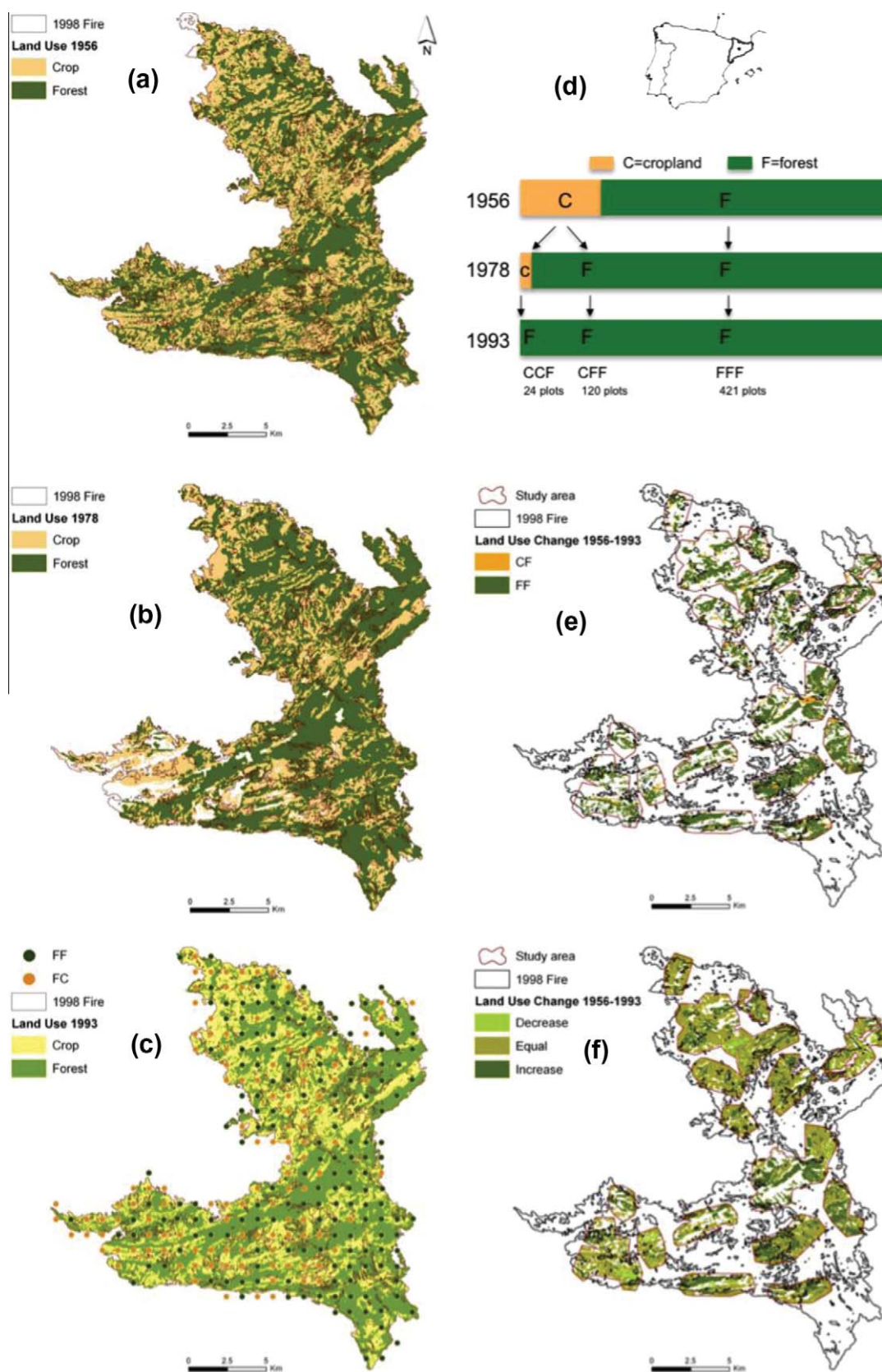
Fig. 1. Historical land use changes and forest cover from 1956 to 1993 in the 1998-fire study area (note that the remaining 1994-fire area is absent in this figure). (a) Land uses in 1956; (b) land uses in 1978; (c) land uses in 1993; (d) land use changes over time Legend: FFF (never cultivated or cropland abandoned before 1956), CFF (cropland abandoned between 1956 and 1978) and CCF (cropland abandoned between 1978 and 1993); (e and f) sub-sampled area considered for estimation of post-fire forest cover (NDVI computations); (e) land-use changes between 1956 and 1993, categories CF (crop in 56, forest in 93) and FF (forest in 56, forest in 93); (f) forest density changes between 1956 and 1993, categories: decreased, equal, or increase forest cover density. Points indicate the locations of the NFI plots, orange for FC (forest in 1993, and cropland or non-forested area in 2001) green for FF (forest in 1993 and 2001) transitions.

ber (7). These different historical land use trajectories were considered as an estimator of the time since cropland abandonment.

Finally, we evaluated forest cover in 1956 and 1993 in a subsample of the area (the 1998 burnt area Fig. 1), using direct photo-interpretation from aerial photographs. The analyzed area was then classified according to (1) the trajectory of land use between 1956 and 1993 (i.e. $C \rightarrow F$ or $F \rightarrow F$) (Fig. 1f, called land use hereafter) and (2) the variation of forest cover between periods (only for the F areas, Forest density hereafter) using three different classes: high density (>70% of tree cover), medium density (40–70%), low density (20–40%).

Post-fire vegetation regeneration was then estimated using remote sensing vegetation indices (NDVI) as surrogates of vegetation vigor and cover (Zozaya et al., 2011). NDVI values were taken in a date when all the deciduous trees had full-formed leaves (May 19th, 2002). Forest cover was estimated in both North and South aspects because in a Mediterranean-type climate they are the two extreme situations in terms of the main abiotic factors (temperature, soil and air moisture, irradiance, etc.) affecting plant distribution (Blondel and Aronson, 1999; Pausas et al., 1999). NDVI values were extracted from randomly selected points that combined each category of (1) historic land-use trajectory (CF, FF), (2) pre-fire cover dynamics (decrease, stable, increase) and (3) aspect (North/South), at a density of 1 point/ha per category*aspect combination.

2.3. Data analysis

We used log-linear models to analyze the effect of the historical land use trajectory (CCF, CFF, or FFF) and wildfire (burned, unburned) on the presence/absence of each of the tree species considered (*Q. ilex, Q. cerrioides, P. nigra, P. sylvestris* and *P. halepensis*). This log-linear analysis fitted a saturated model to the dataset, considering all interactions, indicated by 123 (1 = fire, 2 = land uses, 3 = presence of the considered species). Here the null hypothesis is that presence of the tree species is independent of fire occurrence and land uses. The effects of fire and land uses on presence of each five tree species can be tested by comparing different fitted models with this one using likelihood ratio tests. We used automatic selection (one, two and three way interactions models are tested successively) to select the best-fitting model. Then, no significant interactions were eliminated to keep the model that includes the least number of interactions necessary to fit the observed dataset (Ordóñez et al., 2006). After choosing the best-fitting model, to test the effect of fire occurrence or land use separately, different chi-square tests were carried out to compare the number of plots with presence or absence of each of the species.

Differences in the density of *P. nigra, P. sylvestris, P. halepensis, Q. ilex* and *Q. cerrioides* (in those plots where they were present) due to the effect of time since abandonment of croplands were analyzed using one-way ANOVAs. The predictor variable was the land use category in 1956 (cropland or forest). We did not consider the trajectory of land uses from 1956 to 1978 because of the scarce number of samples in some of the categories. Data of density were log-transformed before the analyses to meet the criteria of normality.

Statistical differences among land use trajectories in forest cover after fire (estimated from NDVI values) were calculated by resampling subsets of 200 points per combination of land use*aspect and forest density*aspect by using 1000 bootstrap runnings. Then, we calculated the mean and 95% confidence intervals for each category and aspect. When confidence intervals did not overlap we considered significant differences among land-use trajectories.

3. Results

Overall, during the second half of the XX century, the rates of crop abandonment in benefit of the forest have increased in the study area, with a faster rate between 1956 and 1978 than between 1978 and 2001 (Fig. 1). From the 565 plots included in the NFI3 forest inventory carried out in 2001, 75% were yet occupied by forests in 1956, this increased to 94.3% in 1978, to finally reach the 100% in 1993, before fire occurred (Fig. 1).

Concerning the post-fire presence of the five species, in 2001: *Q. ilex* and *Q. humilis* were present in 95% of the plots, while *P. nigra, P. sylvestris* and *P. halepensis* in 75.5% of the plots. Pure forests of *Quercus* and *Pinus* species accounted respectively for 24% and 5.4% of the plots, while the rest (70.6% of the plots) were mixed oak-pine forests.

The presence of non-serotinous pines (*P. nigra* and *P. sylvestris*) was negatively associated with fire occurrence, and was independent of time since cropland abandonment (Tables 1 and 2, Fig. 2a). *P. nigra* was present in 55.4% of unburnt plots whereas it decreased to 32.7% on burnt ones (Fig. 2a). *P. sylvestris* followed a similar trend but more pronounced, namely it was present in 49.7% of unburnt plots and only in 9.2% of the burned ones (Fig. 2). Conversely, the presence of *Q. cerrioides* was associated with time since cropland abandonment but was independent from fire occurrence (Tables 1 and 2, Fig. 2). Presence of *Q. cerrioides* was higher in FFF plots (88.1%) than in the other two categories (80.9% in CCF and 77.5% in CFF) (Fig. 2). The presence of *P. halepensis* and *Q. ilex* was independent of fire occurrence and time since cropland abandonment (Table 1, Fig. 2).

Time since cropland abandonment had a different effect on the density of *Q. ilex*, having higher densities in FFF plots (423 stems/ha, $n = 82$) than in new forests arisen after 1956 (242 stems/ha, $n = 34$) ($F = 7.63$, $p = 0.08$). Conversely, the density of *Q. cerrioides* and the three *Pinus* species was not affected by time since abandonment, reaching similar densities in croplands abandoned after 1956 than in those abandoned before 1956 or never cultivated (*Q. cerrioides*: 255.8 ± 16, *P. nigra*: 546.3 ± 35, *P. sylvestris*: 514.0 ± 40, *P. halepensis*: 443.2 ± 43 stems/ha).

Overall, northern slopes showed higher post-fire recovering than southern slopes (Fig. 3). In the northern slopes, stable forest areas showed higher post-fire vegetation regeneration (thus higher NDVI values), than those that were crops in 1956 and later became forested areas (Fig. 3a). The opposite pattern appear in the southern slopes, with higher NDVI values in areas that were crops in 1956 and then forest in 1993 than those that remained a forest through all this period (Fig. 3a). Interestingly, within the northern slopes forest recovering after fire (estimated from NDVI values) was equivalent whether forest cover had increased or remained

Table 1
Main parameters of the best-fitting log-linear models relating (1) land use trajectories (CCF: crop in 1956-crop in 1978-forest in 1993, CFF: crop(56)-forest(78)-forest(93), or FFF: forest(56)-forest(78)-forest(93)) and (2) wildfire (burned, unburned) with the presence/absence after fire of each one of the five tree species considered (*Q. ilex, Q. cerrioides, P. nigra, P. sylvestris* and *P. halepensis*). Variables included in the model are: 1 = wildfire occurrence, 2 = time since cropland abandonment, 3 = presence of the species. Independence of two variables is indicated separating them with a coma while interaction between them is indicated by the absence of coma.

Species	Best-fitting model	Person chi square	df	p [*]
P. nigra	13, 2	5.45	6	0.49
P. sylvestris	13, 2	5.54	6	0.48
P. halepensis	1, 2, 3	5.12	7	0.64
Q. ilex	1, 2, 3	8.53	7	0.29
Q. cerrioides	1, 23	6.50	5	0.26

[*] Note that non-significant *p*-values indicate a good fit between observed frequencies and expected frequencies generated by the model.

Table 2

Species presence in relation to fire occurrence and time since crop abandonment. Values of the Pearson chi squared test for the comparison of fire occurrence (burnt, unburnt) and time since cropland abandonment (CCF:crop-crop-forest, CFF:crop-forest-forest, or FFF:forest–forest–forest) on the presence/absence of *Q. ilex, Q. cerrioides, P. nigra, P. sylvestris* and *P. halepensis* are shown. Significant differences at $p = 0.05$ are indicated in bold.

| Species	Fire occurrence			Time since cropland abandonment		
	df	χ^2	p	df	χ^2	p
P. nigra	1	**29.12**	**<0.001**	2	2.97	0.226
P. sylvestris	1	**105.81**	**<0.001**	2	1.78	0.411
P. halepensis	1	0.47	0.829	2	1.75	0.417
Q. ilex	1	0.84	0.361	2	3.21	0.201
Q. cerrioides	1	0.30	0.581	2	**16.25**	**<0.001**

similar from 1956 to 1993, but substantially higher than those recorded in areas where forest cover had decreased (Fig. 3b). Southern slopes that have increased, decreased, or remained the same in terms of forest cover density, showed no significant differences of post-fire forest recovering (Fig. 3b).

4. Discussion

We found an important role of historic land use changes and fire disturbance (and, more important, the interaction between them)

on post-fire forest recovering in terms of forest cover, species composition and densities. Long-standing forest areas exhibited a higher post-fire recovery and less change in species composition than those previously used in agriculture (i.e. younger forests).

As hypothesized, and first reported by Foster (1992), in our study post-fire species composition – and the associated functional traits – depended on previous land uses. Overall, the abundance of *Quercus* sp. was more heavily influenced by time since cropland abandonment than by fire occurrence while the presence of *Pinus* sp. was less conditioned by time since cropland abandonment and more determined by fire. Although oaks are more abundant than pines in the study area, oaks seem to colonize new areas at a slower speed, owing to the need of secondary dispersers such as Eurasian jay (*Garrulus glandarius*) or several species of mice (mainly *Apodemus sylvaticus* and *Mus spretus*). The same pattern is likely to appear in other biotic plant-frugivorous interactions requiring some degree of forest structure and/or shelter to attain effective seed dispersal (Castro et al., 2010; Gómez-Aparicio et al., 2009; Rost et al., 2009; Lehouck et al., 2009; Uriarte et al., 2011). Indeed, dispersal limitation has been proposed as more critical than recruitment limitation for the colonization of old-forest-specialized plant species after agriculture abandonment (reviewed in Hermy and Verheyen, 2007). Furthermore, animal-dispersed species have often the most habitat-restricted requirements thus
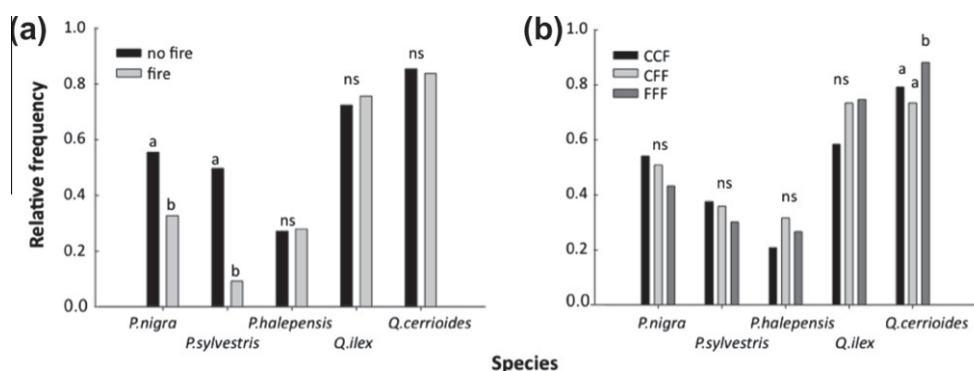
Fig. 2. Presence of *P. nigra, P. sylvestrys, P. halepensis, Q. ilex* and *Q. cerrioides* attending to fire occurrence (a) and time since abandonment (b). Different letters indicate significantly different values at $p = 0.05$ according to the Pearson chi-square test; ns indicates no significant differences. $N = 565$.
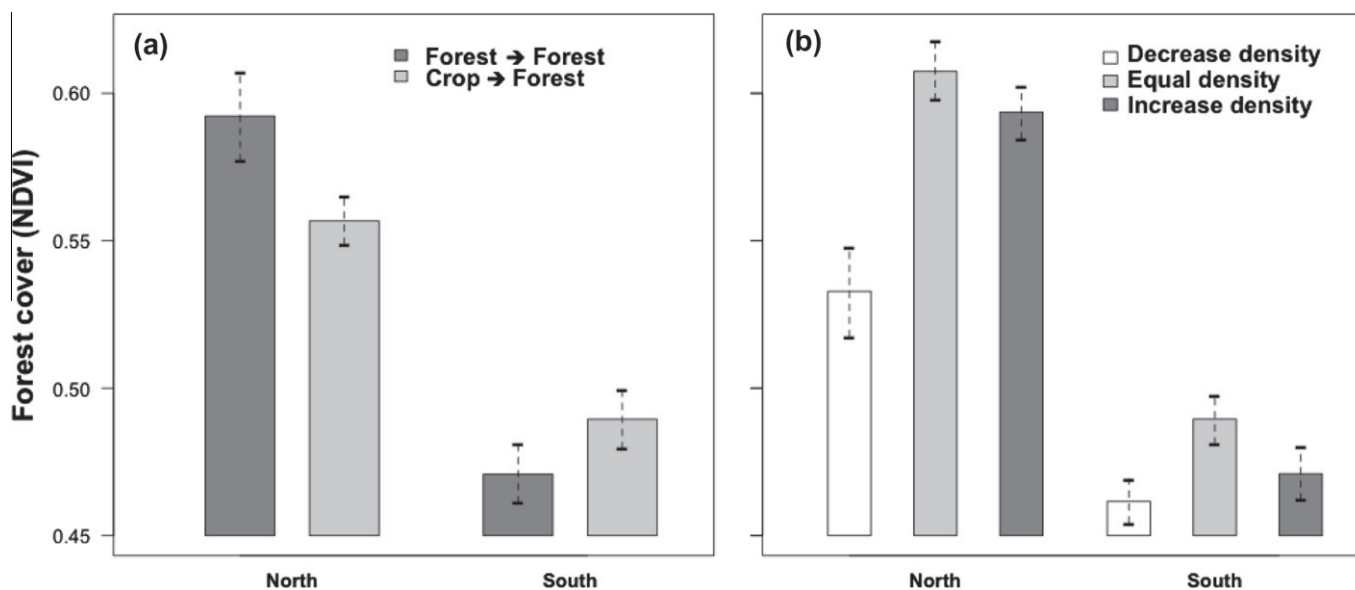
Fig. 3. Forest cover after fire (estimated by NDVI) in relation to land use change (a), changes in forest density (b) and aspect (North vs. South). Whiskers and dashed lines identify confidence intervals at 5% after 1000 bootstrap re-sampling over 200 NDVI focal points at each category*aspect combination (see methods).

it is reasonable if they need more time to disperse seeds into abandoned fields (Uriarte et al., 2011; Lehouck et al., 2009). Conversely, wind-dispersed *Pinus* species can successfully colonize recently abandoned areas (Ordóñez et al., 2006), and this faster establishment capacity – at a shorter period than the years between consecutive aerial photographs used for this study – is supported by the fact that *Pinus* sp. densities did not vary along land use trajectories. Although whether this situation is general for other wind-dispersed species as well is still uncertain (Foster, 1992; Soons and Heil, 2002).

Forest recovering after fire substantially varied according to pre-fire plant composition and cover dynamics. Species with resprouting ability (i.e. *Quercus* sp) dominated post-fire ground surface, while the establishment of post-fire non-resprouter species (*Pinus* sp) depended on the presence of seed sources nearby the burnt area or in their capacity to maintain a canopy seed bank resistant to fire. This species turnover and losses in biodiversity compared to old-grown forests have been reported in many other studies (Trabaud and Lepart, 1981; Pausas et al., 1999; Retana et al., 2002; Rodrigo et al., 2004; Duguy and Vallejo, 2008; among others). The lack of influence of fire occurrence on the presence of *Q. ilex* and *Q. humilis* may be explained by the high resilience they exhibit to burning, through vigorous resprouting from the root collar (Espelta et al., 2003). Indeed, both oak species are able to survive and resprout even after repeated burning (e.g. three consecutive wildfires in less than ten years in Bonfil et al., 2004). Differences in recovery between pines associated to specific traits appeared very clearly, with the presence of those species without a canopy seed bank resistant to fire (*P. nigra* and *P. sylvestris*) being negatively associated with fire occurrence. On the contrary, the presence of *P. halepensis*, that have a fire resistant canopy seed bank (i.e. including serotinous cones), was independent of fire occurrence and time since cropland abandonment, as found in previous studies (Pausas et al., 1999; Rodrigo et al., 2004). It is important to note that the two fires studied in this work were large and massive-crown fires that hindered the arrival of seeds from not burned areas (Ordóñez et al., 2006; Rodrigo et al., 2004). Furthermore, it also seems that, in areas that were cultivated in the past and that recently became *Pinus* spp forests, the post-fire regeneration and forest cover were reduced compared to the long-term forested areas. Overall, while land cover was mainly occupied by *P. nigra* and *P. sylvestris* forests before fire events; after the disturbance, *Quercus* species dominated the landscape (Rodrigo et al., 2004; Arnan et al., 2007). Hence, fire acted as a drastic mechanism of turnover between one group of species and the other as found in former studies (Foster, 1992; Pausas et al., 1999; Puerta-Piñero et al., 2012; Rudel et al., 2005).

Our results suggest that the longer the time since crop abandonment, the more heterogeneity in species and diversity of functional responses to potential perturbations are present, as previously reported (Rudel et al., 2005; Fraterrigo et al., 2006; Hermy and Verheyen, 2007), which thus increases the probability of rapid post-fire forest regeneration. Apart from the presence of nearby seed sources, the regeneration of a burnt area seems to depend either in the presence of fire-resistant soil and canopy seed banks or in the presence of species with resprouting ability (Rodrigo et al., 2004). All these crucial traits that assure the potential resilience of forests to fire are widespread among Mediterranean species (Paula et al., 2009). Within this framework, long standing forests with higher number of species and thus, more diverse in functional traits ensuring forest recovery after fire will have a higher resilience after this intense disturbance (Thompson et al., 2009; Puerta-Piñero et al., 2012; FAO et al., 2008; Walck et al., 2011).

In this study, we found the recovery of burnt sites to be significantly worse in the southern slopes compared to the northern ones. Therefore, we should also consider that some of the patterns

that we found could be constrained by other environmental factors (Arnan et al., 2007; Pausas et al., 1999). In the Mediterranean Basin, for example, marked differences exist between the type of vegetation growing in northern and southern slopes, the latter mainly dominated by drought-tolerant species which are able to survive under high rates of evaporative demand (Zavala et al., 2000; Pausas et al., 1999; Kutiel, 1997). Abiotic factors the years following the fire, such as temperature or water availability, could substantially vary among different parts of the landscape. Furthermore, topographic factors such as elevation, slope or aspect could also play a major role, particularly in areas characterized by harsh climates (Pausas et al., 1999; Kutiel, 1997; Broncano et al., 2005).

On the whole, our findings highlight that predictions on how extensive disturbances such as fire affect the regeneration and further distribution of plants, should take into account also historical land trajectories. In the light of global change a key challenge will be to anticipate the impacts of disturbances on ecosystems. We could point out the need of increasing the diversification of the forests and promoting the presence of woody resprouters (e.g. in conifer monocultures) to help the system to progressively acquire a self-capacity to respond to natural or human-induced disturbances.

Acknowledgements

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