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Post-fire regeneration patterns of *Pinus nigra* in a recently burned area in Mount Taygetos, Southern Greece: The role of unburned forest patches

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ABSTRACT

Pinus nigra (black pine) is an ecologically and economically important species widely distributed around the Mediterranean Basin. *P. nigra* ecosystems have recently been affected by high severity fires occurring over the mountainous forest ecosystems of Southern Europe. The aim of this study is to investigate the post-fire regeneration patterns of black pine after a high severity crown fire which occurred on Mt Taygetos in Southern Greece. A network of 18 sites was selected to study black pine natural post-fire regeneration. Regeneration density was higher at the edges of patches that have remained unburned within the periphery of fire (0.406 individuals/m^2) as compared to isolated burned areas (0.007 individuals/m^2) although a significant between sites heterogeneity was recorded. Boosted regression trees analysis was used to explore the effects of environmental and microhabitat variables on black pine post-fire regeneration. The number of fires a site has experienced had a negative effect on regeneration density, while the presence of recovering ferns had a positive effect. The most important variable related to the black pine post-fire regeneration was distance from unburned patches. The result of the current study substantiates the importance of maintaining fire-resistant stands with large trees that are more likely to survive after a surface fire and which can also serve as seed sources for the recolonization of the burned area after severe crown fires.

1. Introduction

Pinus is one of the oldest genera of the plant kingdom. Today, more than 100 species belong to *Pinus*, making it the richest gymnosperm genus in the northern hemisphere (Mirov, 1967; Vidakovic, 1991; Scaltsoyiannes et al., 2009). Along the Mediterranean Basin, nine species of the genus *Pinus* can be found, representing an important vegetation component that covers more than 13 million hectares across a broad gradient of altitudes (Barbéro et al., 1998). It has been suggested that the periodic occurrence of fire has favored the expansion of pines (Quézel, 1980; Thanos and Marcou, 1991; Agee, 1998; Richardson and Rundel, 1998). In order to understand the current pattern of pine distribution their evolution in relation to fire must be taken into account (Keeley, 2012).

Although fire is thought to be an important ecological factor associated with pine-dominated forest ecosystems, not all pine forests share the same fire regime (Agee, 1998). According to Keeley (2012) pines can be classified into two main groups. The first group comprises species that are distributed in environments where fire is not a regular environmental feature and are characterized as fire-avoiders. The second and largest group includes fire-adapted species commonly found in fire-prone landscapes. Nevertheless, no species can be considered as fire-adapted in general; plant species are adapted to a particular fire regime (Pausas and Keeley, 2009).

Pinus nigra J.F Arnold (black pine) is a fire-resistant tree species provided that it is exposed to low intensity surface fires (Fulé et al., 2008; Touchan et al., 2012). Bark thickness is considered the main trait related to the species' resistance to fire (Tapias et al., 2004), although post-fire survival is also influenced by tree age and the level of crown and stem damage (Ordóñez et al., 2006; Fernandes et al., 2012). *P. nigra* appears to endure fire return intervals (FRIs)

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ranging from 30 to 750 years (Leys et al., 2014), although it can withstand FRIs shorter than 30 years (Christopoulou et al., 2013).

On the other hand, during the recent decades there is an increasing trend of high severity crown fires occurring in black pine forests in the western (Ordóñez et al., 2005; 2006; Fernandes et al., 2008) and eastern part of southern Europe (Kakouros and Chrysopolitou, 2010; Christopoulou et al., 2013). This trend may pose a threat to the existence and conservation status of black pine, especially under scenarios of global warming, which are projected to profoundly affect wildfire frequency and intensity (Moriondo et al., 2006; Giannakopoulos et al., 2009; Fyllas and Troumbis, 2009).

P. nigra does not maintain a canopy seed bank (Habrouk et al., 1999; Ordóñez et al., 2005), so its regeneration after crown fires relies on surviving local seed sources, which may be rare or nonexistent (Trabaud and Campant, 1991; Retana et al., 2002; Ordóñez et al., 2004; Ordóñez, 2004; Pausas et al., 2008). The natural post-fire recovery of burned stands depends almost exclusively on long-distance seed dispersal from neighboring unburned patches or sparse surviving individuals of the species (Retana et al., 2002; Ordóñez and Retana, 2004; Ordóñez et al., 2005; 2006; Arianoutsou et al., 2010). Nevertheless, the dispersion of seeds to the burned area does not necessarily imply an adequate recruitment (Retana et al., 2012). A number of abiotic and biotic factors, such as vegetation and soil cover (Trabaud and Campant, 1991), intra- and inter- specific competition (Trabaud and Campant, 1991; Ordóñez et al., 2006) and post-dispersal seed predation (Ordóñez and Retana, 2004; Kerr et al., 2008) can strongly mediate black pine post-fire recruitment.

The aim of the current study was to investigate the post-fire regeneration patterns of *P. nigra* in the Taygetos mountain range at Southern Greece, which was heavily affected by the 2007 high severity crown fire, which was one of the most extreme natural disasters in the country's recent history (Koutsias et al., 2012). The specific objectives of the study were: (1) to examine the role of unburned stands in the re-establishment of *P. nigra* in burned areas through seed dispersal and (2) to explore the effects of environmental variables and microhabitat characteristics upon black pine seedlings and saplings densities. The results of this study are expected to support restoration and fire management practices in *P. nigra* forests.

2. Materials and methods

2.1. Study area

Mount Taygetos is the highest (2407 m) and longest mountain range of the Peloponnese, Southern Greece. Coniferous forests cover the altitudinal zone between 800 and 1600–1700 m and are dominated by *P. nigra* J.F. Arnold and *Abies cephalonica* Loudon (Greek fir). The main geological substrates are limestone and phyllite-quartzite (Bornovas and Rondogianni-Tsiambaou, 1983). A meteorological station situated near the study area (Touristiko Taygetou 1310 m above sea level), reported a mean annual temperature of 10.8 °C and mean annual precipitation of 983.4 mm for the period between 2010 and 2012. Black pine forests on Mount Taygetos have experienced frequent fires during the last 165 years, with the two most extensive events taking place in 1998 and 2007 (Christopoulou et al., 2013) and being probably promoted by drought (Sarris et al., 2013). Approximately 45% of the area covered by *P. nigra* and mixed *P. nigra – A. cephalonica* forests was burned in the 2007 fire, while 340 ha of black pine forest had also been burned in the 1998 fire. The most abundant understory species in the post-fire communities was the perennial herb *Pteridium aquilinum*. Other common herbaceous species were the annuals *Trifolium campestre, T. angustifolium, Vicia sativa, Aira elegantissima, Bromus sterilis, Briza maxima, Cerastium candidissimum* while perennial species such as *Brachypodium retusum, Achillea nobilis* and *Verbascum* sp. were also common. The most abundant woody species were *Quercus coccifera, Erica arborea, Rubus* sp., *Cistus creticus, C. salvifolius* and *Genista acanthoclada*. Trees such as *Castanea sativa, Quercus ilex, Q. pubescens* and *Fraxinus ornus* were also occasionally present. *A. cephalonica* had practically a null presence because of it lack of any direct adaptation to fire (Arianoutsou et al., 2010; Ganatsas et al., 2012).

2.2. Selection of study sites and sampling

A network of 18 sites was established to study post-fire black pine regeneration (Fig. 1), by applying a remote sensing and GIS-based approach that is described in Supplementary Material. We initially delineated the 2007 fire as well as the unburned stands within the fire perimeter using a high resolution (60 cm) QuickBird color satellite image. This information was subsequently analyzed by applying a set of rules to identify potential recolonization areas (Fig. S1). Twelve (12) of those sites were adjacent to unburned patches (sites A), while six sites were established in isolated (sites I) burned areas. Nine sites (out of 18) were affected only by the 2007 fire, while the rest were also burned during the 1998 fire.

Abiotic and biotic variables such as slope, aspect, altitude, the dominant understory plant species as well as the presence of snags and other woody remnants were recorded for each study site. For the 12 sites selected at the edges of the unburned patches, stand characteristics such as the number of mature trees and the maximum height and the mean diameter at breast height (DBHm) were also measured.

Black pine seedling and sapling densities were measured in alternating plots of 1 m^2 located along three belt transects (100 m long) established in each of the 18 sites. For the 12 sites near the edge of unburned patches the starting point of transects was adjacent to the outermost surviving tree. Recruits that were bearing only the cotyledons were characterized as seedlings, while all other individuals were characterized as saplings. The age of saplings was assessed by the number of nodes (Oreshkin et al., 1997). A total of 10,800 plots were sampled over a three-year long period, starting from April 2010 to September 2012. Because each site was sampled only once, and measurements were performed over sequential years, black pine recruits were considered the result of the seed dispersal that took place in the corresponding post-fire year. This is because black pine does not form any kind of soil seed bank and thus seedlings established in one year originate only from seeds dispersed during the same year. For instance, realized dispersal of 2008 corresponds to black pine individuals that emerged from seeds dispersed in 2008 and they are denoted as RD08.

In each plot the presence and the cover of herbaceous and woody species, fallen branches and trunks, stumps and snags, stones or rocks, litter and bare soil were recorded in a semiquantitative scale (Table 1) with 0 representing cover <25%, 0.5 representing cover >25% and <75% and 1 representing cover >75%. Among the herbaceous species, resprouting ferns (*P. aquilinum*) were very abundant in almost all plots, so they were recorded separately. Fallen branches and trunks, standing burned trees and logs are different types of coarse woody debris (cwd) (Harmon et al., 1986) and they have been aggregated in one group for further analysis.

2.3. Data analysis

For all analyses the recorded number of seedlings and saplings represents the regeneration density of black pine (individuals/m^2) at the study sites of interest. The aspect, the latitude and the slope

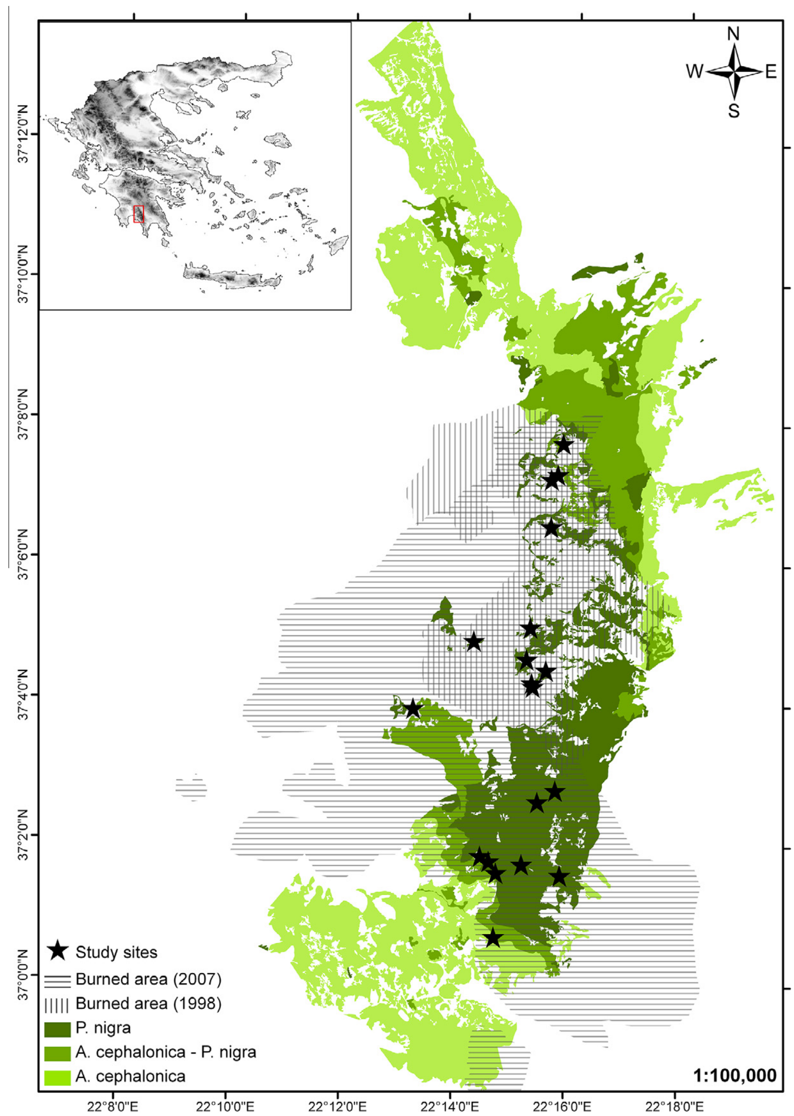

Fig. 1. Location and terrain of the study area (thumbnail). Dominant vegetation types and burned areas and study sites.

Table 1
Explanatory variables used in the BRT analysis.

Variable	Description; units or scale of each variable are provided in parenthesis	Mean (and/or range of values)
Quantitative variables		
Distance	Distance to unburned patches (m)	(0–100)
alt	Altitude (m a.s.l.)	1300 (1075–1460)
hl	Heat load (−1 to 1)	0.98 (0.70–1.04)
sd	Soil depth (cm)	7.46 (1.5–26)
Nt	Number of mature surviving trees (individuals)	93 (2–300)
HNt	Height of mature surviving trees (m)	18.5 (7.22–28.02)
DBHm	Mean Dbh of surviving trees (m)	0.43 (0.22–0.81)
n_fires	Number of fires	(1–2)
Semiquantitative/qualitative variables[a]		
Fern	Cover of ferns[b]	(0–1)
Herbs	Cover of herbs[b]	(0–1)
Woody	Cover of woody species[b]	(0–1)
cwd	Cover of coarse woody debris (includes fallen branches and trunks, stumps and snags)[b]	(0–1)
bs	Bare soil[b]	(0–1)
s_r	Cover of stones and rocks[b]	(0–1)
li	Cover of litter[b]	(0–1)

[a] All semiquantitative/qualitative variables were recorded per plot.
[b] 0 = cover <25% (absence), 0.5 = cover >25% and <75% (intermediate presence), 1 = cover >75% (presence).

of sites were used to compute a heat load index (McCune and Keon, 2002; McCune, 2007). Heat load (HL) provides an adimentional measure of the sites potential drought stress. The term potential is used to distinguish heat load from actual drought stress, as meteorological (e.g. cloud cover, atmospheric coefficient; McCune and Keon, 2002) and ecological parameters (e.g., soil type and shading) were not taken into account for its computation (Fyllas et al., 2008).

Regeneration density as a function of the distance from unburned patches was used as an estimation of the realized dispersal of the study species. Eight empirical dispersal models (Bullock et al., 2006) were comparatively evaluated regarding their ability to fit the data based on the Akaike Information Criterion (AIC) (Dytham, 2011). The model that better represented the data was the one that yielded the lowest AIC.

As a second step data were aggregated into four distance classes: (A) distance < 10 m, (B) 10 m ⩽ distance < 50 m, (C) 50 m ⩽ distance < 100 m and (D) distance ⩾ 100 m. In order to explore the spatial patterns of regeneration density a mixed effect model with distance class as a fixed effect and site as a random component was fitted to the data. Transect variation that is nested within sites was also treated as random. Confidence intervals for both the fixed and random effects were estimated with a bootstrap method of 100 iterations.

Boosted Regression Trees (BRT) analysis was used to explore the effects of environmental and microhabitats variables on black pine post-fire regeneration. BRT is a relatively new statistical method which draws on insights and techniques from both statistical and machine learning methods (Elith et al., 2008), and has been proved very useful for analyzing complex ecological data (Buston and Elith, 2011), including post-fire tree seedlings recruitment (Johnstone et al., 2010). The advantages of BRT are that they can accommodate any type of variable (continuous, categorical, nominal etc.), missing and non-independent data and can also deal with many loss functions (Gaussian, binomial, Poisson etc.), while interactions between predictors can also be qualified and visualized (De'ath, 2007; Elith et al., 2008; Buston and Elith, 2011).

We applied the BRT analysis as described in Elith and Leathwick (2013) using the "dismo" package in R. Two important parameters are the learning rate (LR) and the tree complexity (TC). The learning rate controls the contribution of each tree to the growing model, while TC determines the interactions taken into account (Elith et al., 2008; Buston and Elith, 2011). By changing these two parameters the number of trees (NT) required for optimal model fit are calculated. The bag fraction (BF) was used to control model stochasticity (Elith et al., 2008). In our case the BRT parameters for optimum model behaviour were set as following: LR = 0.005, TC = 3, BF = 0.5 with a Poisson distribution. We started our analysis by fitting BRTs in a stagewise way, starting with the full set of the hypothesized explanatory variables (Table 1) (Johnstone et al., 2010). Model evaluation was performed with cross-validation (CV) in order to estimate the optimal number of trees. CV provides a means for testing the model on withheld portions of data, while still using all data at some stage to fit the model (Elith et al., 2008), and it is an adequate way for predicting error estimation when the data sets are relatively small (De'ath, 2007). We then eliminated variables in reverse order of their relative influence, until subsequent elimination caused a notable (⩾2%) increase in prediction error (Johnstone et al., 2010). Results were interpreted by examining the relative influence of variables and plotting the partial dependencies of responses to individual predictor variables (De'ath, 2007; Elith et al., 2008; Johnstone et al., 2010). Pairwise interactions between predictor variables and their relative strength were also tested (Elith et al., 2008).

All statistical analyses were performed in the R statistical environment (R Development Core Team, 2012).

3. Results

3.1. Size and structure of Pinus nigra regenerating population

A total number of 2952 black pine seedlings and saplings were recorded in all study sites. At the edges of unburned patches mean pine density was 0.406 individuals/m^2 (4060 individuals/ha), with median density varying from 0.000 to 0.500 individuals/m^2. Mean regeneration density was higher near the unburned patch (d < 10 m) compared to all other distance classes (Table 2; Fig 2a). Five years after fire, the regeneration in the completely burned areas remained practically nil, with a mean density of 0.007 individuals/m^2 (70 individuals/ha). A great variability in recruitment density between A-sites (adjacent to unburned patches) was observed (Fig. 2b). The highest black pine regeneration has been reported in Site A12 where 688 black pine seedlings and saplings were measured (mean density = 1.147 individuals/m^2), while the lowest has been reported in Site A01 with a total of 44 black pine seedlings and saplings and mean density being equal to 0.073 individuals/m^2. The density of black pine regeneration did not varied significantly among completely burned study sites (I sites) with the total number of black pine individuals per sites ranging between 1 and 8).

The majority of black pine recruits (72.4%) were the result of the first two post-fire years seed dispersal and germination processes (2008 and 2009), denoted as RD08 and RD09 and accounting for 43.4% and 28.3% of total recruits respectively (Fig. 3).

3.2. Empirical dispersal models

Four of the eight empirical dispersal models tested adequately described the realized dispersal of black pine seedlings and saplings, at the 12 sites established at the edges of the unburned patches. Based on the Akaike Information Criterion (AIC) the mixed function $ae^{-bx} + cx^{-dx}$ yielded the optimum model for describing our data (a = 0.640 ± 0.090, b = 0.016 ± 0.003, c = 1.112 ± 0.112 and d = 0.073 ± 0.014). The same model was also used to describe the realized dispersal for each one of the post-fire years separately (Fig. 4).

3.3. Influence of environmental and microhabitats variables

The final BRT model had 10 variables with an estimated relative importance > 3% and explained 42% of the dataset's deviance. The distance from unburned patches was the most important factor driving black pine regeneration, with a relative influence higher than 30% (Fig. 5). The number of fires and the presence of ferns had a moderate effect on the population density of *P. nigra*, followed by heat load, altitude and DBHm of the surviving trees, while presence of herbs, cwd, soil depth and number of mature trees had a relatively weak effect.

Partial dependencies plots from the fitted model (Fig. 5) indicate that, after accounting for the effect of other variables, the regeneration density of *P. nigra* decreased with increasing distance

Table 2
Results of the mixed effect model reported along the mean and median regeneration density. Different letters show significant differences between distance classes.

Distance classes	Results of comparison	Mean density (individuals/m^2)	Median density (individuals/m^2)
A < 10 m	*a*	1.37	1.00
10 m ⩽ B < 50 m	*b*	0.42	0.00
50 m ⩽ C < 100 m	*b*	0.20	0.00
D ⩾ 100 m	*b*	0.01	0.00

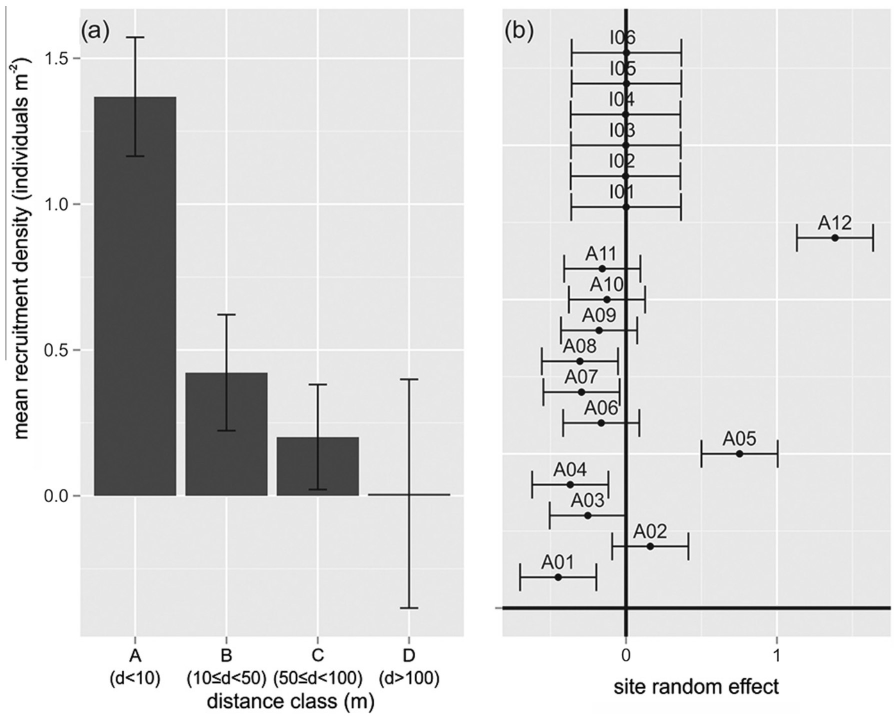

Fig. 2. (a) Mean *P. nigra* recruitment density in four distance classes [distance (d) measured in meters] from the edges of the unburned patches. (b) Site random effect estimated from the mixed effect model showing a significant between sites heterogeneity. A-sites indicate sites adjacent to unburned patches, I-sites indicate isolated sites.

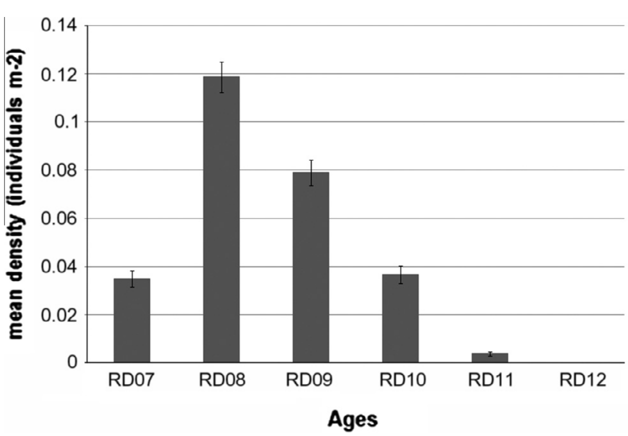

Fig. 3. Inter-annual variation in *Pinus nigra* regeneration density (individuals/$m^2 \pm$ SE). Each barplot represents the result of the realized seed dispersal and germination (RD) from 2007 to 2012.

from the edges of the unburned patch (in accordance to the dispersal model). Black pine regeneration was higher in sites exposed to only one fire event, while recruit density was higher at microhabitats with an intermediate presence of ferns (unimodal relationship). High *P. aquilinum* cover had a negative impact on recruitment density. Intermediate values of heat load seem to favor the establishment of black pine recruits, with altitude having counterintuitive positive effect. Regeneration density was positively related to DBHm of the surviving trees up to a point, after which this effect flattens out. A similar pattern was observed at the partial effect of the number of surviving trees, although the relative influence of this variable was much lower. Regeneration density was lower in plots highly covered by herbs, whereas the presence of black pine recruits was higher in microhabitats covered by fallen branches and trunks, stumps and snags. Finally, soil depth had a negative effect on pine regeneration with higher densities at sites with rather shallow soils.

Distance from unburned patches was also included in three out of five significant interactions identified in the BRT analysis. Important interactions were found between distance from the edge of the unburned patch and ferns abundance, DBHm of surviving trees and number of fires. In summary, the results found suggest that *P. nigra* regeneration is expected to be higher within short distances from unburned patches that contain many large trees and at microhabitats with an intermediate presence of ferns that have burned only once. Other interesting interactions were found between herbs and soil depth and between heat load and altitude, which may explain the notably decrease in black pine density observed in medium altitudes where very high values of heat load were computed.

4. Discussion

Fire is a natural component of Black pine forest ecosystems (Leys et al., 2014). *P. nigra* is a fire-resistant tree species provided that it is exposed to low intensity surface fires (Fulé et al., 2008; Touchan et al., 2012), even if they are recurrently occurring (Christopoulou et al., 2013). Nonetheless, in cases of large and severe fires its post-fire recovery depends mainly on seed availability as the species is not serotinous (Habrouk et al., 1999; Ordóñez et al., 2005; Dodson and Root, 2013). The results of the current work, in agreement with other studies (Retana et al., 2002; Ordóñez and Retana, 2004; Ordóñez et al., 2005; 2006), confirm the importance of unburned patches for the recolonization of burned areas through seed dispersal. Mean *P. nigra* regeneration density in sites near the edges of unburned patches was 0.406 individuals/m^2 (4060 individuals/ha), and showed significant heterogeneity among different sites, ranging from 0.073 to 1.147 individuals/m^2, as also highlighted in Fig. 2b. High variation in *P. nigra* regeneration density has also been reported in other field studies (Trabaud and Campant, 1991; Gracia et al., 2002; Retana

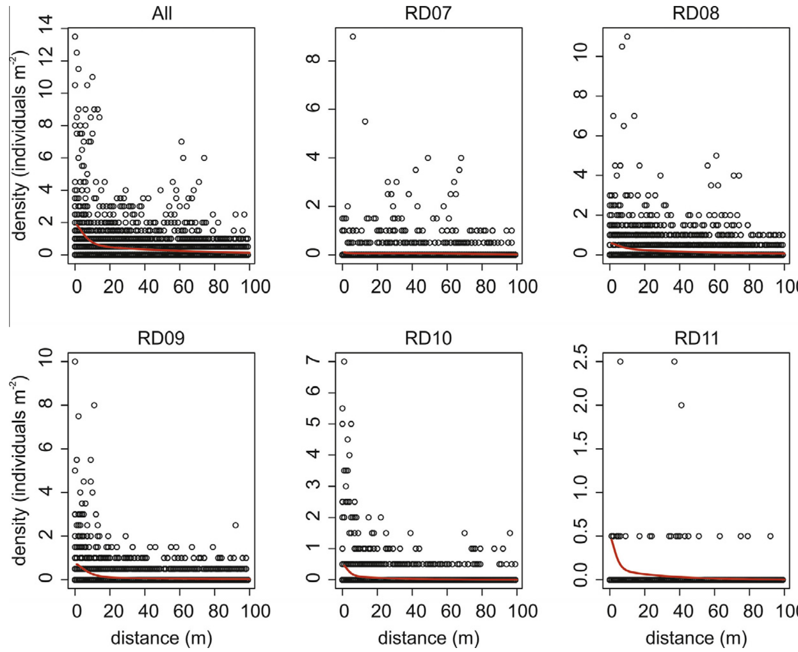

Fig. 4. *Pinus nigra* density along increasing distances from the unburned patches. The red line summarizes the fit of the mixed function $ae^{-bx} + cx^{-dx}$. The first diagram represents the overall mean density, while the other five diagrams represent the result of the realized dispersal for the five consecutive post-fire years.

et al., 2002; Tavşanoğlu, 2008). Ordóñez et al. (2006) have also predicted similar values of regenerating *P. nigra* density in their modelling approach. In our case, at the severely burned areas, five years after fire natural regeneration remains extremely low, with a mean density of 0.007 individuals/m^2 (70 individuals/ha), ranging from 0.000 to 0.500 individuals/m^2. The density of seedlings and saplings is similar to those found for black pine forests in the western [0.022 individuals/m^2 (Retana et al., 2002)] and eastern [(0.077 individuals/m^2 (Tavşanoğlu, 2008)] Mediterranean.

Black pine seedling and sapling density declines with increasing distances from the edges of the unburned patches. *P. nigra* seeds have articulate wings (Klaus, 1989) a typical structure of wind-dispersed pines (Nathan et al., 2001). Similar to what has been reported for *Pinus halepensis* (Nathan et al., 2000; Nathan and Casagrandi, 2004; Nathan and Ne'eman, 2004), seed dispersal shows a peak close to the seed source, followed by a rapid decline and a long tail. The mixed function empirical dispersal model was found to best describe the realized seed dispersal, as expressed through the recorded recruitment density in the current study. Mixed dispersal models assume both local and long-distance dispersal (Clark et al., 1999). Although the spatial pattern of regeneration density may also be the result of secondary seed dispersal regulated by abiotic factors such as elevated stream flow after winter rains (Hampe and Arroyo, 2002) and transport of seeds by predators such as rodents and ants (Ordóñez and Retana, 2004), most studies report that the majority of the seeds disperse within distances shorter than 10 m from the edges of the unburned patch, with long distance dispersal being a rather rare event (Trabaud and Campant, 1991; Ordóñez et al., 2006). The results of the current study show that half of the seedlings and saplings are found within the first 20 m from the edges of the unburned patches, while 75.6% of black pine recruits occur within 50 m of unburned forest.

Most of the saplings recorded in our study (72.4%) were 5 or 4 years old, indicating that the establishment of seedlings starts just after fire (Gracia et al., 2002; Ordóñez et al., 2006). The observed interannual variability in regeneration density can be attributed to the interannual variation in cone and seed production. Kerr (2000) reported that *P. nigra* subsp. *laricio* has the capacity to produce seeds every year, but good seed years occur only every 3–5 years. Large fluctuations in cone and seed production are also reported for *P. nigra* populations in Spain (Ordóñez et al., 2006; Cerro et al., 2009; Tíscar and Linares, 2011a; 2011b), while masting has also been documented for other mountainous conifer species in Greece (e.g. *Abies cephalonica*; Politi et al., 2009). Nevertheless, as previous studies suggest (Ordóñez et al., 2006), a good or a bad year of cone and seed production does not affect significantly the dispersal distance, but rather the number of seedlings established (Fig. 4).

In our study, recolonization in twice burned sites was low, despite the presence of surviving trees. Lower black pine regeneration in twice burned sites seems to be related to local habitat conditions, with twice burned sites being potentially drier (Gracia et al., 2002), or dominated by strong competitors for light such as *P. aquilinum* or perennial grasses such as *B. retusum* that could lead to the depletion of soil nutrients (Gaudio et al., 2011b). *P. aquilinum* regenerates strongly through resprouting after fire (Hofmann et al., 1998; Moretti et al., 2002), and is known to be a strong competitor for light and other resources (Gaudio et al., 2011a; 2011b). Competition with other species is an important factor that can reduce black pine regeneration. Our results agree with those of Trabaud and Campant (1991) that recorded a limited regeneration in sites highly covered by herbs. Ordóñez et al. (2004) also suggested that grasses and shrubs have a major negative impact on the survival of seedlings, directly attributed to resource competition and allelopathy or indirectly to environmental modifications in a way that is detrimental to black pine. Similar results have also been found for other pine species such as *Pinus ponderosa*, where competition with grasses seems to negatively affect regeneration (Dodson and Root, 2013). On the other hand, the presence of shrubs can facilitate pines regeneration and seedling survival (Ordóñez et al., 2004; Dodson and Root, 2013). Nonetheless, according to Tíscar and Linares (2011b) the way shrub species could affect *P. nigra* regeneration depends on both species identity and shrub capacity to colonize new areas. Only specific shrub species such as *Juniperus* spp. seem to facilitate black pine

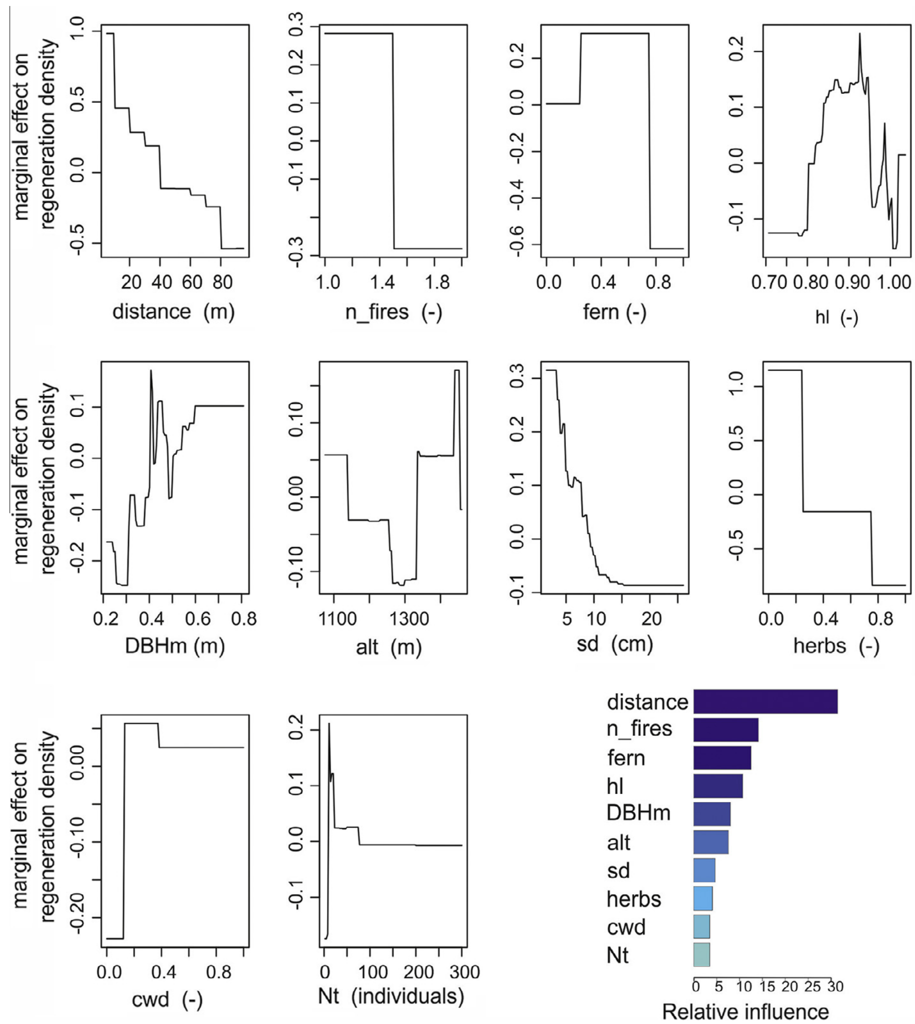

Fig. 5. Partial dependence plots and relative influence of the ten most influential variables affecting *P. nigra* regeneration density (individuals/m^2). A description of the explanatory variables can be found in Table 1.

establishment (Tíscar and Linares, 2011b). In our study the most abundant understory species was *P. aquilinum*. Intermediate abundance of *P. aquilinum* seems to favor black pine density (''nursing effect''), while increased abundance has a strong negative impact. Gaudio et al. (2011b) reported a negative impact of increasing *P. aquilinum* density on *Pinus sylvestris* seedling height growth, with no effect recorded on seedling survival.

P. nigra seedling and sapling density was higher in microhabitats with fallen branches and trunks covering the soil surface, as well as in places with stumps and snags left by foresters. Similar results have also been reported for *P. halepensis* (Pausas et al., 2004; Poirazidis et al., 2012). Fallen branches and trunks, standing burned trees and logs are different types of coarse woody debris (Harmon et al., 1986). Coarse woody debris reduces erosion and favors soil development, stores nutrients and water and provides a source of energy and nutrients (Harmon et al., 1986; Harmon and Hua, 1991). The positive impact of coarse woody debris seems to be associated with provision of ''safe sites'' at the surrounding ground that protect seedlings and saplings from high temperatures and excessive water loss.

Higher values of *P. nigra* density recorded in microhabitats with rather shallow soils seem counterintuitive. Although black pine is found on a range of soil types, including dry and shallow ones, its development is better in deeper soils (Van Haverbeke, 1986). Lower recruitment in deeper soils could be related to higher abundance of other plant species that may be more competitive than pines at this stage of development. For example, perennial grasses develop a dense root system at the same depth as pine seedlings that could lead to stronger competitive interactions (Gaudio et al., 2011b). This is also supported in our BRT results by the interaction found between herb's abundance and soil depth.

Heat load and altitude have also a strong effect on *P. nigra* regeneration density. Intermediate values of heat load seem to favor black pine presence as has also been reported in other studies (Ordóñez et al., 2004; Cerro et al., 2009) that suggest a higher seedling survival and a better growth under moderate light and temperature conditions Although *P. nigra* can withstand high radiation (Tíscar and Linares, 2011a), drought stress as expressed by increased heat load has a negative impact on its density (Fyllas et al., 2008). Patterns of black pine post-fire regeneration in relation to altitude are more difficult to interpret, as many environmental conditions covary with altitude (Körner, 2007). In our case, the altitudinal range of our study sites (1075–1460 m) does not permit solid conclusions in terms of the effect of altitude on pine recruitment density.

Although microhabitat characteristics and environmental variables have diverse effects on *P. nigra* regeneration, the most important determinant of its post-fire regeneration is the existence of unburned patches. According to the BRT analysis, the size of surviving trees as expressed by DBHm is another important factor positively influencing post-fire regeneration. As previously documented by Ordóñez et al. (2005), large trees provide a greater and more frequent cone/seed production than smaller ones, resulting in an increased seedling establishment (Ordóñez et al., 2006). A sufficient number of mature trees within the unburned stand is essential for seed production and dispersal and consequently for successful post-fire regeneration of *P. nigra*. However, the advantage of high tree number is reversed in very dense stands. Dense stands are characterized by lower cone and seed production, a fact that can be attributed to less photosynthetic surface and more limited access to resources for fruit development due to increased intra-specific competition (Arista and Talavera, 1996). Ordóñez et al. (2005) reported similar results for *P. nigra* where both cone production and the proportion of years that each tree produced cones decreased in very dense stands.

5. Implications for management

The results obtained can provide important guidelines for management of black pine forests as well as for other forest ecosystems with similar ecological characteristics, by taking into account the expected future increase in fire activity. In cases of extended crown fires, spatial identification of low regeneration/vulnerable areas would be of key importance for allocating restoration practices. Removing dead trees and coarse woody debris from the landscape should be avoided as apart from soil protection they can also provide suitable microhabitats for successful black pine regeneration.

Mature *P. nigra* tree survival is decisive for post fire regeneration. *P. nigra* stands with large trees are more likely to survive after a surface fire (Fernandes et al., 2012) and can also serve as post-fire seed sources. Large and severe fires will tend to eliminate *P. nigra* from the landscape. Consequently, if the prospects of tree survival are low, then an important management issue could be the ability to maintain fire resistant stands though appropriate understory fuel treatment. Treatments that could decrease fuel biomass, such as stand thinning, selective understory removal, moderate grazing or even prescribed burning, could lead to low intensity or patchy burning in the event of a wildfire. Thus, even under more frequent fires, expected following drier future climatic conditions, *P. nigra* may persist in the long-term provided that an adequate seed source remains at the landscape (Leys et al., 2014).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.05.006.

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