Relative size to resprouters determines post-fire recruitment of non-serotinous pines

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ABSTRACT

The persistence of non-serotinous pines in Mediterranean forests can be threatened by climate-mediated changes in fire regimes that may favor the dominance of resprouters or other fire-adapted species. Recovery of non-serotinous pines after large wildfires is often determined by their ability to grow under the canopy of promptly established resprouters. Mechanisms of facilitation or competition between resprouters and pines will thus have a profound effect on forest dynamics. We examined here the effect of neighboring oak resprouts on *Pinus nigra* Arn. ssp. *salzmannii* saplings 18 years after a wildfire. We determined the net outcome of interactions between oaks and pines and how they vary with the life stage and size of the interacting plants or the environmental conditions. We did not find any net facilitative effects of oaks on pine sapling growth. The sensitivity of pines to neighbors varied markedly with pine size, and to a lesser extent, with water availability during the growing season. Our findings suggest a self-reinforcing hierarchical process by which early-dispersed seedlings growing in low-competitive microsites can grow faster, mitigating neighboring competition in the later stage of canopy closure. These results entail a potentially critical role of management practices to promote post-fire recovery of non-serotinous pines under expected changing conditions of disturbance regimes.

1. Introduction

Wildfires are considered the most important natural disturbance in Mediterranean forests, driving vegetation successional processes and structuring heterogeneous landscapes (Lloret et al., 2002; Pausas, 2015; Trabaud, 1994). Many tree species in Mediterranean ecosystems present adaptive traits that allow them to persist in areas burned with high intensity and take advantage of favorable early post-fire conditions (such as the reduced competition for resources) to develop and grow (Buhk et al., 2006; Paula et al., 2009; Sánchez-Pinillos et al., 2016). This is the case of many species that are able to resprout quickly from surviving parental tissues (persistence of individuals) or that present persistent seed banks (e.g. serotinous pines) (Pausas and Keeley, 2014). In contrast, some obligate seeder species lack efficient mechanisms to rapidly regenerate after fire (Buhk et al., 2006; Lloret, 1998; Retana et al., 2002). In such cases, post-fire regeneration is subject to the resistance of species to fire or to their ability to disperse from distant surviving seed sources (Christopoulou et al., 2014).

In mixed stands composed of resprouting species and non-serotinous

seeders, the former usually recruit immediately or shortly after the fire, while seeders arrive later if the aforementioned favorable conditions are met. Thus, seeder persistence will ultimately depend on the species' ability to co-exist with or replace the first established species (Gracia et al., 2002; Ordóñez et al., 2004; Ordóñez et al., 2006). Once seeder species arrive at a site where resprouter and/or serotinous species are already present, post-disturbance forest dynamics strongly depend on the interactions among individuals growing close to each other. Positive and negative interactions may occur simultaneously between two neighbor plants. The net outcome of unbalanced interactions determines mechanisms of facilitation or competition (Armas and Pugnaire, 2005; Holmgren et al., 1997), and may vary with the life stage and size of the interacting plants or the environmental conditions (Callaway and Lawrence, 1997). In harsh environments such as semi-arid or Mediterranean sites, positive effects often prevail in first stages of plant development (seedling survival and initial growth) (Castro and Zamora, 2004; Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006). However, the large size reached by resprouters for being rapidly established after fire may work against the performance of late-

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established seeders if asymmetric competition occurs. That is when large individuals compete for resources disproportionally with smaller neighbors (Weiner and Thomas, 1986). Furthermore, extremely severe conditions may exacerbate the competitive effects of resprouters (i.e. their ability to suppress the growth of their neighbors) when resources are limited (Maestre et al., 2009; Michalet et al., 2006). Therefore, depending on the sensitivity of seeders to competition (i.e. their competitive response), one could expect that certain species acting as nurse plants during the establishment process might turn into competitors and determine forest dynamics in advanced stages (Schupp, 1995; Sthultz et al., 2007) or during stress periods (Kitzberger et al., 2000; O'Brien et al., 2017).

Mixed pine-oak forests are common forest types in Mediterranean basin, usually conformed by a pine-dominated overstory, and an understory composed of oaks and other resprouting species. While most Mediterranean pines are considered fire-prone species that shortly colonize open areas after disturbances, Spanish black pine (*Pinus nigra* Arn. ssp. *salzmannii*) lacks serotinous cones and only forms transient soil seed banks that are unable to resist the harsh environmental conditions resulted from the wildfire. In contrast, coexisting oaks usually resprout vigorously and become the dominant species immediately after fire (Retana et al., 2002). Consequently, pine recruitment after fire, and therefore the maintenance of the pine-oak mixture, is conditioned to the presence in the landscape of unburned pine forest patches that act as seed sources (Christopoulou et al., 2014; Martín-Alcón et al., 2015) and to the ability of pines to establish and grow under the net interacting effects of the resprouting oaks.

Given the increased drought and heatwaves predicted for the coming decades and the associated increase in fire risk, the persistence of these mixed forests (and particularly of some pine populations) could be compromised (Retana et al., 2002; Rodrigo et al., 2004; Vilà-Cabrera et al., 2012), leading to monospecific communities with lower ability to respond to drought or multiple disturbances (Niinemets and Valladares, 2006; Sánchez-Pinillos et al., 2016). Therefore, understanding interspecific interactions between these two functional groups at different tree life stages is crucial to guide prompt management practices focused on fostering forest resilience.

In this study, we assess the factors affecting the performance of saplings (height between 0.5 and 2.5 m) of black pine (*P. nigra*) growing under oak resprouts 18 years after a wildfire occurred in Central Catalonia (Spain). The main goal of this study is to assess the effect of neighboring trees on pine sapling growth in order to get useful insights into the coexistence mechanisms of post-fire pine-oak communities. Specifically, we address the following questions: (i) What is the net effect (facilitative or competitive) of neighboring resprouting oaks on the growth of black pine saplings and how does this effect change with oak size and distance to target pines? (ii) Is the effect of neighboring oaks mediated by the size of pines? (iii) Is the effect of neighboring oaks mediated by water availability during the growing season?

We hypothesized that the net effect of neighboring oaks would be more negative for large than for small pines, which could be favored by the shadow of larger neighbors. We also expected that competitive effects would be particularly important in dry years under conditions of limited water availability.

2. Material and methods

2.1. Study area

The study was carried out in a central zone of Catalonia (Northeast Spain) (41°52′ N; 1°36′ E) affected by a large wildfire that burned 27,000 ha (two thirds of which woodlands) in 1998 (Fig. 1). The study area locates at low slope areas and altitudes ranging from 575 to 860 m a.s.l. The climate in this zone varies from dry-subhumid to subhumid Mediterranean (according to Thornthwaite index), with a mean annual precipitation of 589.9 mm and a mean annual temperature of 13.6 °C.
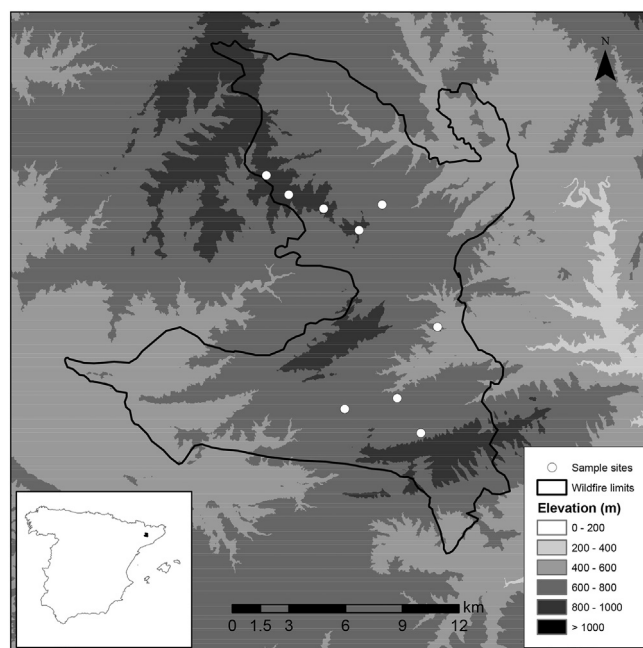

Fig. 1. Location of study sites within the perimeter of a fire occurred in central Catalonia (Northeast Spain).

Previous to the wildfire, this region was mainly occupied by Spanish black pine in pure natural stands or dominating the overstory of two-layered stands, with resprouting species (mostly deciduous sub-Mediterranean oaks) growing in the understory (Gracia et al., 2000). The wildfire triggered a wide resprout of hardwood species that are now dominant in most of the affected area, with some disperse individuals of black pine that regenerated from close unburned patches (Martín-Alcón et al., 2015; Puerta-Piñero et al., 2012). The most abundant hardwood species are *Quercus pubescens* Willd., *Quercus faginea* Lam., and the hybrid *Quercus subpyrenaica* E.H. del Villar (*Q. faginea × Q. pubescens*), whereas some individuals of holm oak (*Quercus ilex* L. ssp. *ballota*) can also be found. Common box (*Buxus sempervirens* L.), Kermes oak (*Quercus coccifera* L.), and blackberries (*Rubus* sp.) can be found in the understory of oak forests.

2.2. Field sampling

During spring 2016, we selected nine sites, separated between each other by at least 1.5 km to cover different environmental conditions within the 1998 wildfire perimeter (Fig. 1). Stands were selected for being currently dominated by resprouting tree species close to unburned patches of black pine (within 50–100 m), avoiding sites where salvage logging and tree plantings were carried out. We selected 183 target pine saplings with basal diameters ranging between 1 cm and 6 cm and total height between 0.70 and 2.40 m (Appendices Table A1). For each target pine, we considered as neighbors all trees growing closer than 3 m, and we also sampled neighbors between 3 and 4 m from the target whenever they presented a diameter at breast height (*DBH*) greater than 7.5 cm. For each tree (targets and neighbors), we measured its basal diameter (*BD*) and total height (*H_t*). We also measured the horizontal distance between trunk bases of each target pine and its neighboring trees (*dist*).

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.009.

We measured primary and secondary growth of all targets for the last five years (2012–16). Primary growth (i.e. height growth) was obtained by measuring inter-shoot separations, whereas secondary growth (radial growth) was measured from basal disks after harvesting the target pines in autumn 2016. We defined radial growth of target

trees as the mean basal area increment at the tree base (BAI_b) of the last five growing seasons (2012–16). We also estimated the age of all target pines by counting the number of tree rings at the tree base. To approximate neighbor size at the beginning of the considered growing period (2012), we randomly selected 78 oaks distributed across the study area such that sampled oaks presented a basal diameter distribution similar to that of target pine neighbors. We then cut down and measured radial growth at the tree base of the sampled oaks. Radial tree ring increments were measured to a precision of 0.01 mm by means of a Lintab 3 measuring system coupled to a TSAP tree-ring software (Rinn, 1996).

2.3. Growth models

Following traditional distance-dependent analyses of competition (Canham et al., 2004; Coates et al., 2009), we modeled pine tree growth as a function of (i) target size, (ii) target age, and (iii) target's neighborhood, defined by the amount, sizes and distances of neighboring trees:

$$NCI_i = \sum_{j=1}^{n} \frac{size_j^\alpha}{dist_{ij}^\beta} \quad (1)$$

The Neighborhood Competition Index (*NCI*) quantifies the net effect of neighbors assuming that the competitive impact of a neighboring tree (*j*) on each focal pine (*i*) with *n* neighbors increases with neighbor's size ($size_j$) and decreases with the distance ($dist_{ij}$) between the focal pine (*i*) and each neighbor (*j*). Parameters α and β determine the importance of size of and distance to neighbors on competition, respectively, and allow for non-linear effects of these variables on NCI. Therefore, we modelled the expected value of log growth of individual trees as:

$$\log(BAI_b) = A + B\cdot\log(NCI) + C\cdot\log(Size) + D\cdot\log(Age) + \varepsilon \quad (2)$$

where A, B, C, D, α and β are the estimated parameters.

We considered separately two variables of tree size measured before the study period (i.e. 2012): basal area and total height. We tested models including all possible combinations of explanatory variables (Table 1), after ensuring that they were not highly correlated (Pearson's correlation coefficients < 0.7). Parameter values were estimated through simulated annealing (Goffe et al., 1994), using the *likelihood* package (Murphy, 2015). We used Akaike's information criterion corrected for small sample sizes (AIC_c) to decide whether the candidate explanatory variables (size, age and competition) were important predictors of tree growth. An explanatory variable was only considered as a good predictor if including that variable in the model resulted in a reduction of AICc of at least two points (Burnham and Anderson, 2002). Model comparison was performed using the *AICcmodavg* package

(Mazerolle, 2016).

2.4. Effects of tree size and inter-annual changes in water availability on tree growth and competitive effects

Once the best model was identified for pine growth (i.e. the *general model*), we evaluated how the competitive effect of neighbors was mediated by the target tree size. For that, we defined two pine size classes and we fitted a model in which parameters were estimated separately for each size class. This approach allowed us to assess variations on the intensity of competition (parameter B) as a function of the size of target trees. In addition, since all NCI parameters are estimated by the model, we could assess how the effects of different components of NCI (i.e. neighbors' size (α) or distance to target trees (β)) vary across target size classes. We compared the resulting model with the general model via AICc.

Additionally, we evaluated the inter-annual variation of each of the predictors of tree growth and its potential relationship with water availability during the growing season. For that, we fitted a model in which we estimated growth for each individual year (instead of for the whole period) considering the variables that better explained pine growth in the general model. We used annual mean growth (BAI_b) of oak trees sampled in the study area to approximate neighbor size (BA at the base of tree stems, BA_b) in previous years and calculate NCI. For that, we calculated log–log relationships between BAI_b and BA_b. Then, we estimated BAI_b for each neighbor as a function of their current size, and approximated their size in previous years by subtracting their estimated annual growth to their current size. In order to avoid potential lack of independence for fitted parameters, we estimated a unique α and β for all years, whereas the rest of parameters were estimated per year. This model was then compared to the general model via AICc.

We assessed the relationship between the effects of the considered variables and inter-annual changes in water availability through linear correlations between model estimates and the Standardized Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010). SPEI was calculated from monthly plot-level meteorological data (mean monthly temperature and monthly precipitation), obtained through interpolation of nearby meteorological stations using the *meteoland* package (De Cáceres et al., 2018). We calculated SPEI for the whole growing season (i.e. from March to November) and considering the period 1990–2016 to state normal climatic conditions. We used the *SPEI* package (Beguería and Vicente-Serrano, 2013) to calculate SPEI. All analyses were performed in R (R Core Team, 2016).

3. Results

3.1. Growth models

The best model of pine sapling growth included competition by neighboring trees (NCI) and initial pine BA_b as explanatory variables and explained 64% of the variation in individual tree growth (Table 1). Although the model including age as an additional variable presented equivalent support (ΔAIC_c = 1.88), we selected the former for being more parsimonious. In general, pine sapling growth was better predicted through explanatory variables based on BA_b than on height. Specifically, the model including NCI and initial BA_b had a largely stronger support than the analogous model considering height (ΔAIC_c = 88.29; Table 1).

The competitive effect of neighbors (NCI) increased linearly with neighbor size, as inferred by the parameter estimate ($\alpha \approx 1$), whereas it decreased non-linearly with its distance from target tree, stabilizing for distances greater than one meter (Table 2; Fig. 2). The steep decline in pine growth as a function of the neighborhood index indicates that competition by neighbors prevails over any facilitative effect (B < 0; Table 2, Fig. 2). Size-growth relationship displays a non-linear concave curve associated with size-symmetry where growth increases

Table 1
Comparison of all candidate models describing the effect of neighborhood (NCI, Eq. (1)), target pine size (BA_b or Height), and age on pine growth by means of Akaike's Information Criterion (AIC_c), Akaike weights (*w*), the maximum likelihood value found for each model, and goodness of fit (R^2).

Candidate models	AIC_c	ΔAIC_c	w	LL	R^2
$\log(NCI_{BA}) + \log(BA_b)$	214.72	0.00	0.72	−101.12	0.64
$\log(NCI_{BA}) + \log(BA_b) + \log(Age)$	216.60	1.88	0.28	−100.98	0.64
$\log(BA_b)$	226.17	11.45	0.00	−110.02	0.60
$\log(BA_b) + \log(Age)$	228.24	13.52	0.00	−110.01	0.60
$\log(NCI_H) + \log(Height)$	303.01	88.29	0.00	−145.27	0.41
$\log(NCI_H) + \log(Height) + \log(Age)$	305.68	90.96	0.00	−145.27	0.41
$\log(Height)$	342.23	127.51	0.00	−168.05	0.24
$\log(Height) + \log(Age)$	344.47	129.75	0.00	−168.12	0.24
$\log(NCI_H) + \log(Age)$	346.52	131.80	0.00	−167.02	0.25
$\log(NCI_{BA}) + \log(Age)$	347.21	132.49	0.00	−167.37	0.25
$\log(NCI_H)$	358.78	144.06	0.00	−174.22	0.19
$\log(NCI_{BA})$	358.87	144.15	0.00	−174.27	0.19
$\log(Age)$	382.40	167.68	0.00	−188.13	0.06

Table 2

Maximum likelihood estimates and support limits for parameters of the best model describing the effect of neighborhood (NCI, Eq. (1), and initial target tree size (BA$_b$) on pine sapling growth.

Predictor	Estimate	Lower limit	Upper limit
A	0.89	0.82	0.94
B	−0.24	−0.26	−0.23
α	0.80	0.73	0.86
β	0.49	0.10	0.86
C	0.52	0.52	0.59

$\log(BAI_b) = A + B \cdot \log(NCI) + C \cdot \log(BA_b)$.

See Eq. (1) for α, β.

degressively with pine size (Pretzsch and Dieler, 2011). Additionally, we could detect an interaction between target and neighbor sizes and their effect on target growth. Thus, the increase in pine growth with size was larger as smaller the neighbors (Fig. 3).

3.2. Effects of tree size and inter-annual changes in water availability on tree growth and competitive effects

The model considering two different size classes of pine saplings showed an equivalent support than the best general model ($\Delta AIC_c = 0.19$; $R^2 = 0.65$), and the competitive response of small and large pines was similar (parameter B, Table 3). However, we found a much larger competitive effect of neighbors on small than on large pines. In particular, the effect of neighbor size (α) on the growth of small pines was almost seven times higher than on large pines.

The annual model of tree growth explained 80.9% of the variation and showed lowest effects of both competition and initial basal area at the stem base in 2013, a particularly wet year (SPEI$_{13}$ = 1.45). In contrast, the largest effect of target tree size was observed in 2012, the driest year (SPEI$_{12}$ = −0.40; Table 4). Indeed, SPEI was highly and

negatively correlated with the effect of initial target tree size (Person's $r = −0.85$), and positively correlated with the competitive effect of neighbors ($r = 0.62$), suggesting that the competitive disadvantages of small pines are fostered during drought periods, whereas the competitive effect of neighbors is partially mitigated (i.e. less negative) during the wettest years (Fig. 4).

4. Discussion

The results obtained in this study reflect the main constraints of young black pines growing under high-density forests of oak resprouts more than a decade after a large wildfire. Our analyses revealed that performance of saplings is strongly influenced by their size, and especially by the ratio between their size and that of their neighbors. The sensitivity of pines to neighbors (i.e., their competitive response) varied markedly with pine size, and to a lesser extent, with water availability during the growing season. Our results suggest a self-reinforcing effect by which seedlings dispersed early and growing in relatively low-competition microsites can grow faster and reach sooner large sizes, making them less sensitive to their neighbors' influence during the later stage of canopy closure. In reverse, the pines initially growing in crowded neighborhoods cannot reach this threshold size and are more affected by the competitive effect of oaks throughout their life cycle. All this suggests the importance of certain environmental conditions, temporarily transitory so that the coexistence of pines and oaks can occur in a certain place (Nathan et al., 2013).

4.1. Interdependent effects of size and neighborhood on tree growth

Neighboring effects and the initial size of pine saplings were the main drivers of pine growth during the analyzed life stage (12.8 ± 2.3 years; mean ± sd). We found that the net outcome of interactions between target pines and their neighbors was always
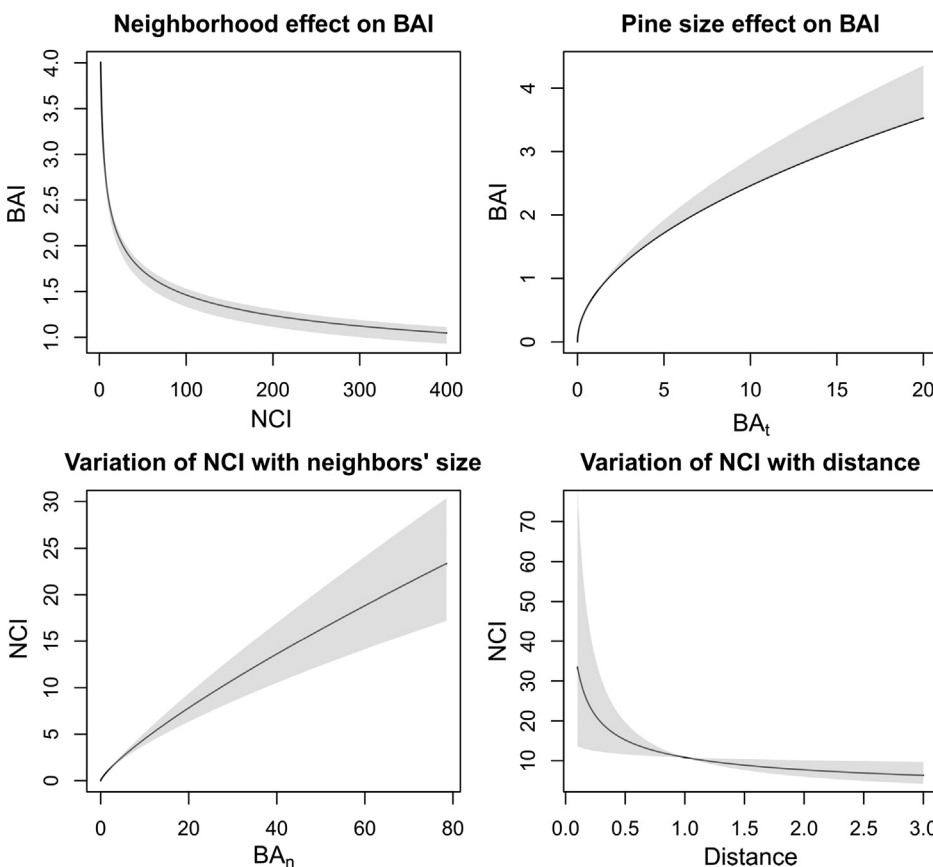
Fig. 2. Model-predicted relationships based on the best growth model (Table 2). Effect of NCI on BAI when the target tree has a basal diameter D = 2 cm (top-left); effect of target pine size (in BA at the tree base) on BAI at an intermediate level of competition (NCI = 140) (top-right); effect of the average size of neighbors on NCI when the target tree has a basal diameter D = 2 cm (bottom-left); and effect of the average distance between the target pine and its neighbors on NCI when the target tree has a basal diameter D = 2 cm (bottom-right). The shaded area shows upper and lower support limits.
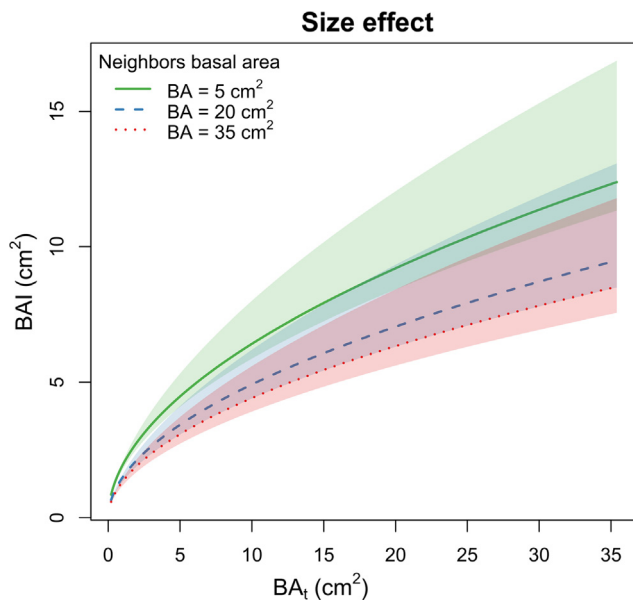
Fig. 3. Influence of initial size of focal pines and neighboring trees on pine sapling growth. BAI was predicted for three neighbor sizes, at 2 m from the focal pine. Initial size was calculated from allometric equations from sampling data. The shaded area shows upper and lower support limits.

Table 3

Maximum likelihood estimates and support limits (in brackets) for parameters of the best model describing the effect of neighborhood (NCI, Eq. (1), and target size (BA_b) on pine growth by considering two size classes.

	Pine size classes	
Predictor	Large	Small
A	0.50	1.29
	(0.41; 0.58)	(1.18; 1.34)
B	−0.22	−0.32
	(−0.25; −0.18)	(−0.35; −0.3)
α	0.11	0.76
	(0.1; 0.21)	(0.71; 0.87)
β	0.13	0.10
	(0.1; 0.87)	(0.1; 0.37)
C	0.42	0.44
	(0.37; 0.47)	(0.32; 0.56)

$\log(BAI_b) = A + B \cdot \log(NCI) + C \cdot \log(BA_b)$.
See Eq. (1) for α, β.

Fig. 4. Variability of estimate values for the explanatory variables (BA at the tree base of target pines, and neighborhood effect, NCI) calculated for each year in 2012–2016. Values reported are the maximum likelihood estimates and the support limits. Dashed lines represent linear relationships between the estimates and SPEI in the five considered years. The effect of BA was negatively correlated with SPEI (r Pearson = -0.85), and the effect of NCI was positively correlated with SPEI (r Pearson = 0.62) (i.e. less negative effect in the wettest years).

competitive. Even more, and in contrast to our predictions, the competitive response of pine saplings was greater for small than for large saplings, completely ruling out the existence of facilitative processes at early life-stages. Although small saplings are more adversely affected by larger neighbors than large saplings, differences are not disproportional to be considered size-asymmetric competition, but rather as partial size-symmetric competition (Pretzsch and Biber, 2010). Size-asymmetric competition is a common process in other Mediterranean pinewoods (Bravo-Oviedo et al., 2006; de-Dios-García et al., 2015), and it is often related with competition for light when tree heights of neighbors and target trees are compared (Schwinning and Weiner, 1998). In contrast, size-symmetric competition is assumed to occur under limiting below-ground resources (Pretzsch and Dieler, 2011). This agrees with the fact that basal area (at the stem base) was more relevant as size variable

Table 4

Maximum likelihood estimates and support limits (in brackets) for parameters of the best model describing the effect of neighborhood (NCI, Eq. (1), and target size (BA_b) on pine growth by considering five years (2012–2016) with different SPEI values.

	2012 (SPEI = −0.40)	2013 (SPEI = 1.45)	2014 (SPEI = 0.98)	2015 (SPEI = −0.30)	2016 (SPEI = 0.25)
A	−1.13	−0.73	−0.43	−0.07	−0.02
	(−1.19; −1.04)	(−0.81; −0.67)	(−0.49; −0.36)	(−0.14; −0.01)	(−0.07; 0.06)
B	−0.11	−0.07	−0.10	−0.16	−0.18
	(−0.12; −0.08)	(−0.09; −0.06)	(−0.12; −0.09)	(−0.18; −0.15)	(−0.19; −0.15)
α	0.58	0.58	0.58	0.58	0.58
	(0.51; 0.64)	(0.51; 0.64)	(0.51; 0.64)	(0.51; 0.64)	(0.51; 0.64)
β	0.50	0.50	0.50	0.50	0.50
	(0.50; 0.85)	(0.50; 0.85)	(0.50; 0.85)	(0.50; 0.85)	(0.50; 0.85)
C	0.81	0.68	0.71	0.74	0.76
	(0.75; 0.85)	(0.64; 0.73)	(0.68; 0.76)	(0.7; 0.76)	(0.73; 0.79)

$\log(BAI_b) = A + B \cdot \log(NCI) + C \cdot \log(BA_b)$.
See Eq. (1) for α, β.

than total height in the general growth models, reflecting that there is higher competition for soil resources than for light in our study area (Pretzsch and Biber, 2010; Schwinning and Weiner, 1998).

The variable effect of neighbors depending on pine size suggests that the intensity of interactions between resprouters and seeders rapidly becomes a self-reinforcing hierarchical process with small trees being more negatively affected by competitive effects of neighbors than large trees. There is also a general pattern found in many forest communities by which tree growth increases proportionally with size up to an intermediate size (about 20 cm in diameter for *Pinus nigra*) from which growth rate declines as size increases (Coates et al., 2009; Gómez-Aparicio et al., 2011). Therefore, there is a feedback effect such that isolated trees, growing faster than trees in crowded areas due to the lower competitive environment and the higher solar radiation (Lucas-Borja et al., 2017), also become larger and further increase their growth because of the larger size itself. In this sense, pine seedlings dispersed early or far away from oak resprouts may rapidly reach larger sizes and suffer less competition than seedlings established close to oaks, particularly if these are larger. This is evidence of how important the existence of certain windows of opportunity for successful pine recruitment is, and underscores the importance of spatially or temporal heterogeneity for the coexistence of pines and oaks in the study area (Valladares et al., 2015).

Our results suggest that the net outcome of positive and negative interactions between seeder and resprouter species shifts soon along the early life states. In Mediterranean areas, seedling survival is often facilitated by small shrubs or a low cover on *Quercus* (see Castro and Zamora 2004, Ordóñez et al. 2004, Tíscar and Linares 2014) as it probably occurs in our sites, allowing the coexistence of both pine and oak regeneration after the fire. However, these facilitative effects seem to disappear for seedling growth (Gómez-Aparicio et al., 2004), and rapidly change into strong competitive effects when pines reach sapling stage. This negative interaction slightly buffers as saplings grow, but the net outcome remains negative throughout the rest of the stage.

Although we did not explicitly compare the interactions among plants belonging to the same species, the decreasing competitive effect of oaks on large pines and the observed stagnation in the growth of oak resprouts (personal observation) make plausible the hypothesis that coexistence of both species can also be mediated by the lower competition among plants belonging to different species than among conspecific plants (Gómez-Aparicio et al., 2011; Zhao et al., 2006). Nevertheless, further research is needed to test this hypothesis.

4.2. Effects of inter-annual changes in water availability

Our results reflect that the intensity of interactions vary annually as a function of overall climatic conditions. The stress-gradient hypothesis states that under water-stress conditions (dry microsites or dry periods), neighboring shade may ameliorate drought effects by reducing plant evapotranspiration (Bertness and Callaway, 1994). Contrarily, we found saplings were more adversely affected by competition during dryer seasons. While neighboring shade may favor understory plants, competition for soil moisture may increase and counterbalance the positive effects (Kitzberger et al., 2000; O'Brien et al., 2017). Accordingly, water limitation during the driest periods seems to aggravate the net competitive effects of neighbors on pine saplings. This result agrees with the refined version of the stress-gradient hypothesis that predicts negative neighboring effects under extremely severe conditions when the stress is driven by a limiting resource as water (Maestre et al., 2009; Michalet et al., 2006)

Furthermore, the positive effect of target tree size was stronger in drier years. This suggests that the hierarchical process resulting from the interdependent effects of size and neighborhood is reinforced, and growing disadvantages of small saplings are fostered under water-stress

conditions. Mediterranean oak species have thick and well-developed root systems that allow them to store carbon and reach water in deep soil layers (Paula and Pausas, 2011). Therefore, pine saplings regenerated after fire must compete for soil moisture with oaks that resprouted from fire-resistant structures belonging to adult trees before fire. As a consequence, under drought conditions in which upper soil layers dry up, only the largest pine saplings may be able to get water efficiently.

4.3. Natural post-fire dynamics and management implications

Our results inform on post-disturbance dynamics of forests composed of species with contrasted responses to disturbances and different competitive abilities. Furthermore, we believe that our results constitute a decision support framework that can be helpful for planning future management actions focused on fostering recovery of non-serotinous seeders after forest fires, and therefore, to favor the coexistence of functionally different species. This study reflects interdependent effects of size and neighborhood on the performance of black pine saplings, and how the intensity of these effects may be hampered by dry conditions. Our results clearly indicate that the success of non-serotinous pine saplings to reach the canopy level and co-exist with resprouters depends on seedling ability to reach a certain threshold size as soon as possible, so that they are able to avoid competitive exclusion until their fitness equals that of oaks. While a certain cover of resprouters may enhance seedling survival during the first stages and be even needed to ensure species coexistence between oaks and pines (Castro and Zamora, 2004; Lucas-Borja et al., 2016), our results agree with previous studies that found this facilitative effect rapidly changed into competition (Gómez-Aparicio et al., 2004). Moreover, the negative effect of resprouting neighbors on pine performance is likely to continue in more advanced stages in the transition from sapling to adult sizes, and can easily lead to competitive exclusion of pines (Vayreda et al., 2013).

These results are especially relevant under future predictions of global change for Mediterranean ecosystems. First, more severe and frequent wildfires will reduce the chances of adult pines to survive and thus, chances of successful dispersal into appropriate resprouter-free microsites. Second, warmer and drier events would intensify neighborhood competition on pine performance, increasing the likelihood of competitive exclusion by oaks. As a consequence, the failure of direct regeneration and the negative effect of resprouters on late-established pines are expected to limit its ability to reach and overtop the resprouter-dominated canopy and thus, decrease the distribution of non-serotinous pines in the landscape at the expense of the overall expansion of resprouters (Martín-Alcón and Coll, 2016; Retana et al., 2002; Rodrigo et al., 2004). This will reduce forest functional diversity, and therefore their resistance and resilience to future combined disturbances (Sánchez-Pinillos et al., 2016).

Results obtained in this study provide useful information to understand the dynamics of mixed pine-oak forest at the mid-term after fire, and allow us to conclude specific management recommendations (Fig. 5). In the absence of silvicultural practices, our results point to a slow recovery of black pine stands to the pre-fire state. Slow recovery times in the context of frequent fire may put pines at risk because they are unable to reach sizes that confer resistance (e.g. minimum bark thickness) or avoidance (minimum canopy height above the flammable resprouter understory) to fire (González et al., 2007; Ordóñez et al., 2005). At high competition intensity, pine growth is retarded until overcoming –if so– resprouters' size. Therefore, to favor pine-oak forests after fire, management should consider prompt thinnings on dense stands dominated by resprouters, but once pine seedlings are established (Lucas-Borja et al., 2012). By eliminating large resprouters located close to the pines (distance < 1.5 m) during the exclusion stage,

Expected stand growth without thinnings

Expected stand growth with thinnings
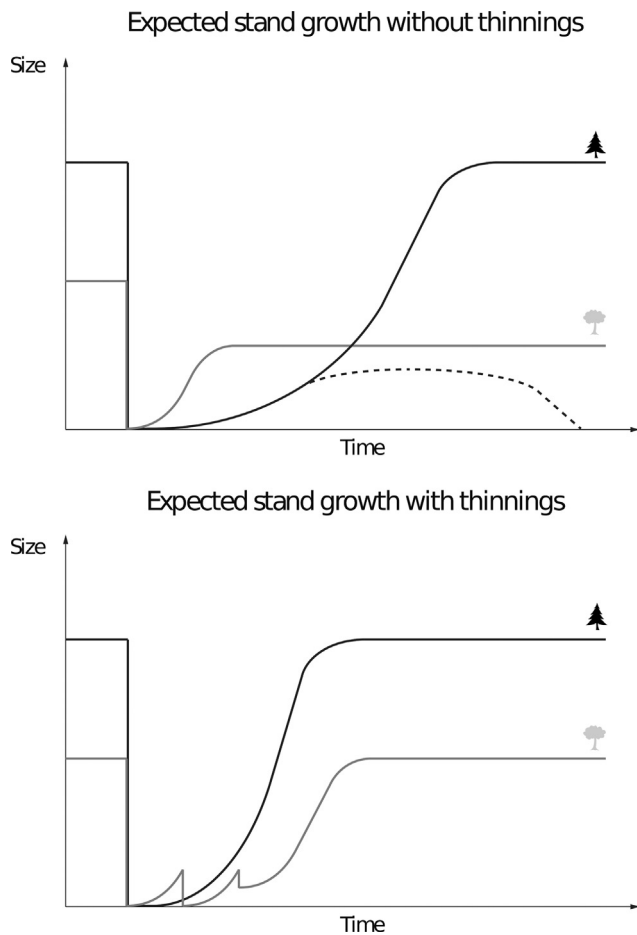
Fig. 5. Expected forest dynamics without (top panel) and with (bottom panel) management interventions. Black and grey lines represent pine and oak dynamics over time, respectively. Basal area of both pines and resprouters sharply decrease due to fire. While resprouters immediately start growing, pines regenerate later. Without intervention, it is expected that pine basal area recovers slowly to the pre-fire state, or even pines might be unable to overcome resprouters (dashed line). Prompt interventions after pine germination are supposed to favor pines and oaks to reach larger sizes and recover early to the pre-fire pine-oak mixed forests.

one can equalize fitness differences between pines and oaks, favoring pine growth until they get a minimum size to avoid competitive exclusion. Post-fire restoration efforts should emphasize large saplings pinpointing relatively open resprouter-free microsites in order to assure rapid pine overtopping.

Acknowledgements

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