Species coexistence in a mixed Mediterranean pine forest: Spatio-temporal variability in trade-offs between facilitation and competition

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ABSTRACT

Studying species coexistence is key to understanding the way in which forests will respond to climate change. We studied the patterns of mixed stands including two main Mediterranean pine species: *Pinus pinaster* Ait. and *Pinus pinea* L. The spatial distribution of adult trees and saplings was studied via a point pattern approach. The effect of competition on growth of adult trees was investigated by comparing the performance of several competition indexes for each pine species through generalized linear models. Adult trees formed mixed clumps in which individuals of both species appeared together. Part of the tree growth variation was explained by tree size along with tree competition. However, the effect of conspecific *vs* heterospecific competition on tree growth differed and reflected species-specific neighbor-asymmetric competition. Facilitation was fundamental in the early stages for tree species development. The spatial distribution of saplings was strongly related to the spatial distribution of adult trees, also being asymmetrically clustered and neighbor-species-dependent. However, the required facilitation in early life-stage trees shifted to competition among trees in the adult stage. Species mixture may be desirable in terms of increasing and diversifying productivity, although the conditions currently present in the stand are likely to lead to future dominance of *P. pinea* over *P. pinaster* due not only to the greater competition tolerance of the former but also to a greater ability to successfully recruit in the plots, forming clusters that may be in turn be impenetrable to *P. pinaster*. Therefore, in order to maintain mixed stands, it would be necessary to enforce adequate silvicultural management strategies which avoid future stand dominance by *P. pinea*.

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1. Introduction

The spatial patterns observed in plant communities have been explained in terms of ecosystem self-organization, resulting from different mechanisms and factors (both direct and indirect as well as their interactions) acting on trees (Law et al., 2001). These mechanisms generate the observed spatial structure in ecological communities (Callaway and Walker, 1997; Koppel et al., 2006). However, the link between processes and patterns is not clear because many processes can create the same pattern (McIntire and Fajardo, 2009; Perry et al., 2006). Although examining a pattern does not allow the specific mechanism that determines that pattern to be identified, some ecological information can, nonetheless, be discerned (Brown et al., 2011; Law et al., 2009). A clumped distribution is an indication of species having similar ecological requirements (Rüger et al., 2009), facilitation among individuals (Barker et al., 1997; Bever, 2002), or dispersal limitations at larger scales (Burslem et al., 2001). Segregation of species reflects different ecological requirements of species, niche partitioning or the existence of a mechanism that prevents the development of a particular species in the proximity of another species (Callaway and Walker, 1997). A regular distribution pattern arises when net competition dominates, causing repulsion between individuals (Stoll and Newbery, 2005).

In addition, the factors which affect the pattern of a species in plant communities could change over the life of the individual,

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given that many species appear to exhibit different ecological habitat preferences over the various life stages (Comita et al., 2007). Moreover, the sign of the interactions may not be constant throughout the life of the individual (Cavard et al., 2011). Furthermore, plant–plant interactions can shift from competition to facilitation when high levels of stress are present in herb and shrub communities (García-Cervigón et al., 2013; Gea-Izquierdo and Cañellas, 2009; Brooker et al., 2008). These notions tie in with the postulated stress gradient hypothesis (Bertness and Callaway, 1994; Maestre et al., 2009), which states that facilitative plant-plant interactions are more important and more intense in high-stress environments, such us arid ecosystems (Bertness and Callaway, 1994). This hypothesis has been tested in Mediterranean arid ecosystems, although with differing conclusions (Lortie and Callaway, 2006; Maestre et al., 2009), hence the question has yet to be resolved.

There is, nevertheless, some evidence of the existence of shifts in intraspecific facilitation/competition in Mediterranean shrub communities (García-Cervigón et al., 2013; Verdú et al., 2010) and mixed Mediterranean tree stands (Peñuelas and Boada, 2003; Zavala et al., 2000). Some species may also be better adapted than others to new environmental conditions, such as intense dry periods (Jump and Penuelas, 2005; Peñuelas et al., 2001). Differences in competition or facilitation responses in relation to climatic variability, along with differences in the spatial organization of the species in a mixed stand may lead to a reduction in coexistence; certain species benefitting more than others, increasing their dominance and thereby modifying the previously mixed stands.

Research and management efforts in Mediterranean forests have often focused on pure stands, despite the fact that mixed Mediterranean forest are complex ecosystems which exhibit greater potential than pure stands in terms of specific and structural diversity (Barbeito et al., 2009) as well as landscaping, resistance and resilience to biotic and abiotic hazards, economic income, optimal biomass production and stand stocking as well as and landscaping and recreational use (Landeau and Landmann, 2008). In the Northern Plateau of central Spain, mixed stands of *Pinus pinea* L. and *Pinus pinaster* Ait have traditionally been favoured (Gordo et al., 2012). The economic importance of these multiple use species lies in the production of edible pine nuts in the case of *P. pinea* and good quality resin in the case of *P. pinaster*. These two species coexist in mixed stands, partially due to the fact that *P. pinea* and *P. pinaster* are quite similar in terms of ecological requirements, although they differ in certain aspects such us the primary dispersal method (Del Peso et al., 2012; Manso et al., 2012). These species coexist in the area in natural or seminatural formations (Gordo et al., 2012).

Recent research undertaken in mixed stands of these species has revealed that both *P. pinea* and *P. pinaster* have severe problems for natural regeneration (Gordo et al., 2012). In the case of *P. pinaster* the main limiting factor is seed survival during the summer of the first year, reducing recruitment almost to zero in these sandy soils, except in the area under the crown where higher moister levels are present (Del Peso et al., 2012; Rodríguez-García et al., 2010, 2011). The main problems for natural regeneration in *P. pinea* are: mast-year occurrence (Calama et al., 2011), seed dispersal limitations and seed predation (Manso et al., 2012). However, under favorable conditions, seedlings can establish and successfully develop under the crowns (Barbeito et al., 2008). Mediterranean ecosystems are threatened due to their sensitivity to new climatic conditions caused by climate change (Benito-Garzón et al., 2008; Gea-Izquierdo et al., 2013; Lindner and Calama, 2012; Ruiz-Labourdette et al., 2012). Hence, it is crucial to determine the main factors allowing tree coexistence in Mediterranean ecosystems.

The aim of the present study is to investigate the arrangement of tree species in mixed P. *pinaster* and *P. pinea* stands in order to gain an insight into the mechanisms which determine tree species coexistence. Through the following analyses, an attempt is made to clarify the spatial strategies of trees that allowed coexistence and competition among them: (1) analysis of the spatial distribution of adult pine trees and whether or not DBH, tree height, crown size and slenderness are spatially structured; (2) tree growth modeling, comparing different competition indices which express different ecological assumptions, analyzing competition involving each species separately and (3) spatial distribution modeling of saplings in relation to adult trees, including alternative spatial covariates.

2. Materials and methods

2.1. Study area and field sampling

Two plots of 1 ha (100 m × 100 m) were installed in late fall 2009 in two mixed *P. pinea*–*P. pinaster* stands located in the Spanish Northern Plateau. Plots were selected in which the proportion of stems/ha and basal area of the least represented species was at least 30%. In each plot, all the adult trees of both species (DBH > 7.5 cm) were positioned (coordinates x, y) and breast height diameter measured as the average of two perpendicular diameters (DBH) was recorded along with total height (h), crown diameter (cw) and height to crown base measured as the average of two perpendicular diameters (hcb). Increment cores at 1.30 m were extracted from all adult trees using a Pressler increment borer. All juvenile trees (h > 1.30 m; DBH < 7.5 cm) within the plot were positioned and marked (Fig. 1). Core samples for 5 dominant trees of each species in each plot were taken. This information was used to calculate the site-quality for both species in the plots. The tree-ring measurement of these trees indicated that they were all aged between 79 and 92 years. The mature trees were naturally regenerated in the area, so the current spatial pattern reflects natural conditions. Some clear cutting may have been carried out, but there is no detailed information available in this regard. In the Íscar area, the management method employed is the floating periodic block method. However, in the plots included in this analysis, no regenerative cuttings have been undertaken, and the current regeneration is due to the natural dynamic of the stand.

2.2. Characterization of the spatial pattern of adult trees

The spatial organization of adult trees was studied through a point pattern analysis approach. To test the null hypothesis of spatial independence among the individuals, the Ripley's univariate K cumulative function (Ripley, 1977) was employed, with the complete spatial randomness null model, along with its non-cumulative o-ring function (Ripley, 1981). The rejection of this hypothesis would imply the existence of either a cluster or a regular pattern, as reflected in Ripley's K function. This function was calculated including (i) all adult trees pooled together; (ii) only *P. pinea* trees; (iii) only *P. pinaster* trees. To assess the spatial dependence between pairs of species, the bivariate K_{rs} function with the toroidal shift null model (Dale, 1999; Van Lieshout and Baddeley, 1999) was employed. The toroidal shift null model simulates independent distribution conditioned on the observed point pattern of both classes, keeping the position of the points of one class unchanged and shifting all the points of the other class by the same random vector, assuming that there is continuity between the upper and lower and between the right and left boundaries of the plot. The toroidal shift null model was chosen because we assumed that the spatial distribution of both species
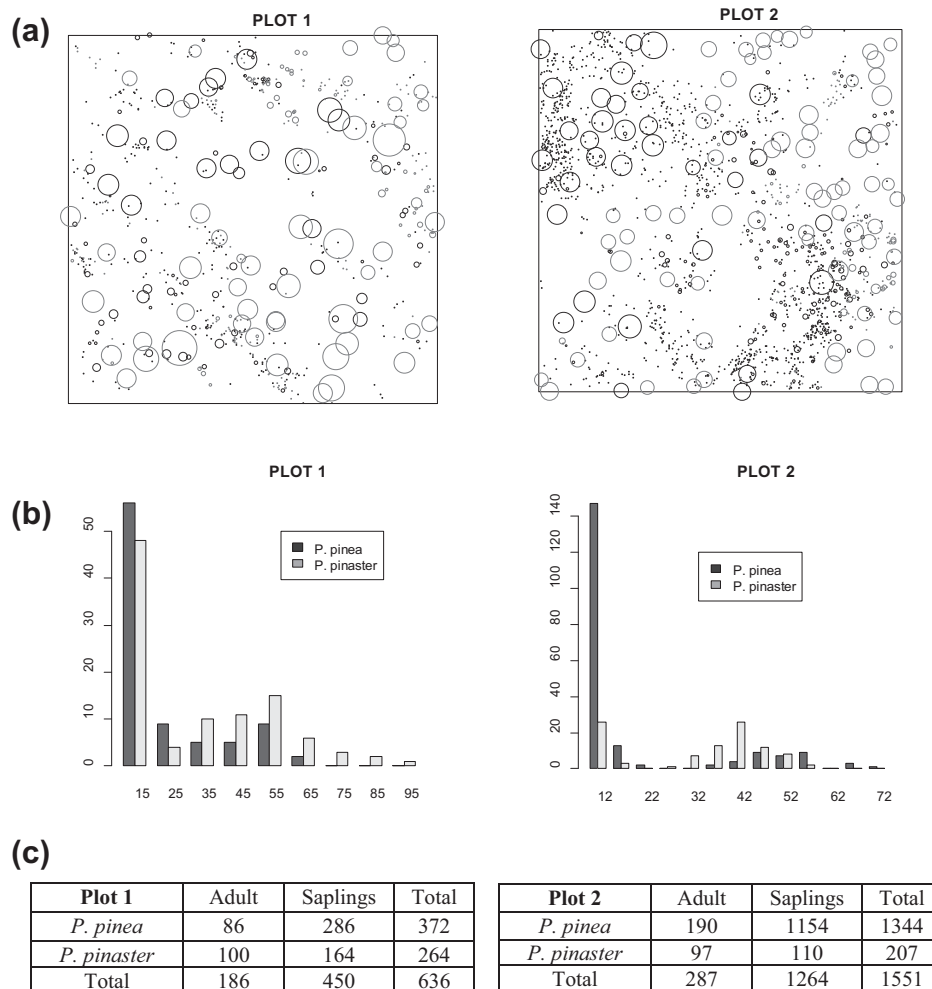
Fig. 1. Measured plots (a) map of the overall woody plant distribution, where each adult tree is represented by a circle with a radius proportional to the tree diameter and the saplings are represented by points. *P. pinea* is in dark grey and *P. pinaster* in lighter grey, (b) diameter distribution of adult trees and (c) number of saplings and adults trees of each species.

and the distribution of saplings and adults were *a priori* independent processes (Goreaud and Pélissier, 2003).

To study the spatial structure of the dendrometric variables (DBH, *h*, cw, slenderness and tree growth), the Stoyan's mark correlation function was used (Stoyan and Stoyan, 1994) to test spatial positive, negative or neutral correlation of the target variables. The random labeling null model was also used because the size characteristics depend not only on age but also on competition, so it might be considered that different growth conditions involve an *a posteriori* process (Goreaud and Pélissier, 2003).

In all cases, 999 iterations were computed to create the null model acceptance band. The error probability in one-sided testing is $\alpha = 1/(K + 1)$, where K is the number of simulations (Illian et al., 2008). A $\alpha = 0.001$ was considered. The maximum distance of analysis was 25 m, which corresponds to 25% of the plot length. The isotropic edge (Ohser, 1983; Ripley, 1981) was used as an edge correction for the aforementioned point pattern analysis functions.

2.3. Modeling tree growth and competition

We used DBH increment over the past 10 years as an explanatory variable to construct empirical models of tree growth. This period is long enough to reduce the interanual climatic variability affecting tree growth in these forests (Gea-Izquierdo and Cañellas, 2009; Calama and Montero, 2005).

Tree growth is primarily related to tree age (or DBH as a surrogate of age), site conditions and competition (Gea-Izquierdo et al., 2013; Pretzsch and Biber, 2010; Biging and Dobbertin, 1995).We used the DBH of trees from ten years ago (to estimate future diameter growth instead of past diameter growth) as a surrogate of age along with different competition indices although site index was not included. We calculated the site quality curves for both *P. pinaster* (Bravo-Oviedo et al., 2007) and *P. pinea* (Calama et al., 2003). These curves gave similar results in both plots. Thus, it was accepted that no differences in terms of site quality existed between the two plots. Nevertheless, we checked whether *P. pinaster* and *P. pinea* diameter increment was significantly different, and confirmed that this was so ($p < 0.01$; *F*-test).

Different neighborhood indices, namely, distance-independent and distance-dependent (Biging and Dobbertin, 1995; Tome and Burkhart, 1989) were compared to determine the most suitable explanatory variable for competition (Table 1). These indices were calculated with individuals of both species together and then for each species separately, in order to assess competition associated with conspecific/heterospecific individuals, considering the tree DBH as the initial tree size, which was DBHt-10; as considered in the growth model. The indices were calculated considering an individual target tree, for which the value for any competition index was calculated in a radius of 5 m and 10 m (for distance independent indices) and considering 3 and then 5 neighbors (for distance

Table 1
List of the different competition indices (CI) calculated and then included in the growth model fitting.

Distance independent		
CI_1	N_5, N_{10}	N
CI_2	BAL_5, BAL_{10} Wykoff et al. (1982)	$BAL = \sum_{i=1}^{N-1} \pi/4 DBH_j^2$, when $DBH_i > DBH_j$
CI_3	$BALmod_5$, $BALmod_{10}$ Schroder and Gadow (1999)	$BALmod = \sum_{i=1}^{N-1} 1 - [1 - BAL_i/G]/HI$
CI_4	SDI_5, SDI_{10} REINEKE (1933)	$SDI = \sum_{i=i}^{N-1} 10^{(\log N + 1.605 \log DBH - 1.605)}$
Distance dependent		
CI_5	CE_3, CE_5 Clark and Evans (1954)	$CE = \left(\sum_{i=1}^{N} r_i/N \right)/(1/2\sqrt{\rho})$ $\quad N = 3; \ N = 5$
CI_6	Hegyi index$_{3,5}$ Hegyi (1974)	$Hegyi = \sum_{i=1}^{N-1} \frac{DBH_j/DBH_i}{r_i};$ $\quad N = 3; \ N = 5$

Five and ten indicated the diameter around the centre of each target tree in with the competition indices were calculated. N is number of trees; DBH_i is the diameter at breast height of tree j; HI is the hart index $HI = 100/H_0\sqrt{N}$; r_i is the distance to the nearest tree; ρ is the stand. In all cases, $i \neq j$.

dependent indices). The averaged value of any competition index was the averaged value of the result for every tree. The Donnelly edge correction (Donnelly, 1978) was used for distance dependent indices.

To define the growth models, we fitted generalized linear models (GLMs) which took the form $[\Delta = DBH = f(\beta_0 + \beta_1 DBH + \beta_2 Comp\ intraespec + \beta_3 Comp\ interespec)]$, that is, we included the competition associated with only conspecific and only heterospecific individuals separately. A Gaussian error distribution was compared to a Gamma distribution. In both cases, the canonical link function was used (i.e. identity for Gaussian, reciprocal for the Gamma model) (McCullagh and Nelder, 1989). The values of the β parameters of the model were estimated using maximum likelihood methods obtained using iteratively reweighted least squares. The different competition indices (Table 1) were included alternatively (Pretzsch and Biber, 2010; Schwinning and Weiner, 1998) and the resulting models were compared.

To evaluate the model, the residual distribution derived from the model was checked by analyzing the following plots to make sure that the desired results were obtained: (i) residual vs fitted values to confirm error independence, (ii) square root (stand residuals) vs fitted values to confirm the equal variance of the errors (iii) the QQ plot to confirm the normal distribution of the residuals.

To validate the model, a cross-validation was carried out by splitting the data randomly into 20 groups of approximately equal size. The GLM was then fitted to the data, omitting each group, and a cost function was calculated between the observed responses of the group that were omitted from the fit and the prediction of the fitted models (Faraway, 2005). Formerly, t-tests were used to determine whether the included explanatory variables were influential in the model. The efficiency of the fitted model was checked and compared with nested models using the Akaike Information Criterion (AIC).

2.4. Modeling spatial distribution of saplings

To study the factors influencing the spatial distribution of saplings, we fitted different inhomogeneous Poisson process models (IPPM) for each species in each plot. The key step in fitting Inhomogeneous Poisson models is the estimation of λ, the intensity or point density (Illian et al., 2008), which we considered to vary according to the explanatory variables included in the IPPM spatial model. We included different variables in λ estimation in order to identify the best explanatory related to adult trees characteristics (DBH, h, cw, growth, slenderness, adult tree density, conspecific

adult tree density, heterospecific adult tree density) with regard to the observed sapling distribution in the plots. Nested models were compared with the AIC.

We used a λ exponential response, $\lambda_\theta(x,y) = \exp(\theta_0 + \theta_1 v_1(x,y))$, where $v_1(x,y)$ was the value of the spatial covariate at point (x,y) and θ were the parameters of the model. We modeled λ in the IPPM using a GLM with a Gaussian error distribution and a canonical link function. For parameter estimation, we used maximum likelihood methods, using the approximate method proposed by Huang and Ogata (1999). Point pattern models require edge correction, so we used the translation correction.

However, trees can display a clumped second-order distribution due to the effects of dispersal (Wiegand et al., 2007). Hence, a spatial component was also included in the λ estimation as a polynomial depending on the x and y spatial coordinates, along with the explanatory variable included in a second approach, $\lambda_\theta(x,y) = \exp(\theta_0 + \theta_1 v_1(x,y) + \theta_2(x,y))$.

We used the Kolmogorov–Smirnov test to evaluate the goodness-of-fit of the fitted IPPM models (Baddeley et al., 2005) under the null hypothesis that the model is true. We also constructed the four-panel plot according to Baddeley and Turner (2005), which includes two graphs of residuals and the lurking variables against the Cartesian coordinates.

To include the aforementioned spatial variables in the IPPM, it was necessary to previously construct an image layer containing the value of the covariate in the plots. For this purpose, we used an ordinary kriging approach (Cressie, 1993), to obtain the values for growth, diameter and height for the plot as a whole using a 5×5 m grid. As P. pinaster and P. pinea could have different growth patterns, the values for growth, diameter and height were normalized for each species in order to obtain the growth, diameter and height value layers.

2.5. Software

All the analyses were conducted using R statistical software (R Development core Team, 2005). We used the spatstats package (Baddeley and Turner, 2005) for the spatial analysis to build the competition indices and to fit the point pattern models using the ppm functions. To fit the glm models and for the cross validation analysis we used the boot package (Canty and Ripley, 2013) and the geoR package (Diggle and Ribeiro, 2007) for the variogram fitting and ordinary kriging.

3. Results

3.1. Characterization of the spatial pattern of adult trees

The spatial pattern of both species was similar. Trees were clustered in the plots, forming clumps of 10–15 m in plot 1 and 15–20 m in plot 2 (o-ring functions, Appendix 1). In addition, the clumps themselves clustered together resulting in a strongly aggregated pattern in the plots ($\widehat{K}(d)$, Appendix 1). The clumps were composed of a mixture of P. pinaster and P. pinea individuals in plot 1, whereas in plot 2, each species tended to remain separate ($\widehat{K}_{rs}(d)$, Appendix 1). As for the spatial correlation of dendrometric variables, the DBH was negatively correlated in the plots ($\widehat{K}_{mm}(d)$, Appendix 1). This implies repulsion between individuals of similar size, probably due to the effect of competition. However, P. pinaster showed stronger negative correlation, indicating that P. pinea may be more tolerant to the presence of neighbors (either conspecific or interspecific individuals) than P. pinaster in mixed stands. As regards height and crown projection areas, the results were similar to those for DBH, although repulsion was less pronounced. Stem slenderness showed positive spatial correlation, as expected; the

greater the number of trees, the stronger the positive correlation ($\hat{K}_{mm}(d)$, Appendix 1). It should be noted that growth was not spatially structured ($\hat{K}_{mm}(d)$, Appendix 1).

3.2. Modeling tree growth and competition

The competition indices calculated (Table 2) revealed that *P. pinea* tolerates a greater number of neighbors when considering either total trees or heterospecific individuals (*F* test, *p*-value < 0.001). However, *P. pintaster* tolerates a greater number of conspecific individuals (*F* test, *p*-value < 0.001).

3.2.1. P. pinaster fitted model

In the case of *P. pinaster*, the most accurate growth model (lower AIC) was obtained using a Gamma error distribution function with the canonical link, including the Reineke SDI index as a competition index, considering an area of influence of 5 m around each tree:

$$\Delta d_{10} = \{1/0.297 + 0.016 DBH + 0.589 SDI(pinea)_5\}$$

With intercept ($p < 0.0001$); DBH ($p < 0.0001$), SDI(pinaster)$_5$ ($p = 0.2131$) and SDI(pinea)$_5$ ($p = 0.0308$). This model explained 53.4% of the total growth variation with a RMSE = 0.395 cm. As can be seen in the model, competition with *P. pinea* was the main factor affecting *P. pinaster* diameter increment.

3.2.2. P. pinea fitted models

In the case of *P. pinea*, the most accurate model was also obtained using a model which included an error following a Gamma distribution with the canonical link, again using the SDI competition index, considering a radius of 5 m. The obtained model was:

$$\Delta d_{10} = \{1/0.337 + 0.004 DBH + 3.542 SDI(pinea)_5\}$$

With intercept ($p < 0.0001$; *t*-test); DBH ($p < 0.0104$), BAL(pinea)$_{10}$ ($p < 0.0003$) and BAL(pinaster)$_{10}$ ($p = 0.3560$). This model explained 20.6% of the total variation (Table 3). As can be seen, the effect of *P. pinaster* was not significant in the *P. pinea* diameter increment model, as might have been suspected from the competition index results.

3.3. Modeling the spatial distribution of saplings

In the case of *P. pinaster* the best IPPM model (in terms of lower AIC) was obtained with a λ that included the spatial density of adult trees as an explanatory spatial variable, both in plot 1 and plot 2 (Table 4). The models fitted in both plots were similar, as expected, and the small differences in parameter θ values may be due to the difference in the number of trees in each plot. *P. pinaster* sapling distribution was found to be positively related to the distribution of adult trees. The seedling density distribution can be seen in Fig. 2a, and the results of the models are presented in Fig. 2c. This

Table 2
Results of the different competition indices averaged for *P. pinea* and *P. pinaster*. The Total column is the average competition index results for all trees of *P. pinaster* and *P. pinea* respectively; the conspecific and heterospecific columns are the average results when only conspecific and heterospecific trees were included respectively.

	Total		Conspecifics		Heterospecifics	
	P. pinaster	*P. pinea*	*P. pinaster*	*P. pinea*	*P. pinaster*	*P. pinea*
Distance independent indices						
N$_5$	2.65	3.71	1.43	2.84	1.22	0.87
N$_{10}$	9.95	13.51	5.06	10.00	4.09	3.51
BAL$_5$	0.06	0.11	5.05	5.04	0.01	0.07
BAL$_{10}$	0.31	0.48	0.25	0.18	0.06	0.30
BALmod$_5$	0.83	0.90	0.36	0.21	3.06	4.33
BALmod$_{10}$	0.84	0.94	0.59	0.46	1.36	1.62
ISD$_5$	0.02	0.03	0.36	0.21	3.06	4.33
ISD$_{10}$	0.84	0.94	0.59	0.46	1.36	1.62
Distance dependent indices						
CE$_3$	1.44	1.32	2.02	1.66	2.36	3.06
CE$_5$	1.81	1.67	2.58	2.09	2.87	3.66
He$_3$	0.18	0.24	0.13	0.27	0.17	0.09
He$_5$	0.06	0.05	0.07	0.17	0.07	0.04

Table 3
Comparison among the parameters of the different fitted empirical growth models for *P. pinaster* and *P. pinea*. LL = logarithm of maximum likelihood estimate; AIC = Akaike Information Criterion; DEV = deviance and RMSE = root mean square error. The most accurate models are in bold capitals.

	Gamma				Gausian			
	−2LL	AIC	DEV	RMSE	−2LL	AIC	DEV	RMSE
P. pinaster								
N$_5$	−146	302	49.36	0.42	−190	390.1	45.57	0.64
N$_{10}$	−146	302	49.36	0.42	−191.2	392.4	44.92	0.64
BAL$_5$	−146	302	49.37	0.42	−191.3	392.5	44.89	0.64
BAL$_{10}$	−148.5	307	48.09	0.43	−193.9	397.8	43.37	0.65
BALmod$_5$	−139.8	289.7	50.79	0.42	−177.1	364.1	49.26	0.62
BALmod$_{10}$	−139.6	289.3	52.24	0.41	−183.1	376.2	48.51	0.62
ISD$_5$	**−53.6**	**117.3**	**54.14**	**0.40**	−68.1	146.2	46.45	0.69
ISD$_{10}$	−115.7	241.5	53.54	0.40	−150.9	311.8	48.01	0.63
CE$_5$	−149.3	308.5	47.69	0.43	−194.4	398.9	43.07	0.65
CE$_{10}$	−149.2	308.5	47.71	0.43	−194.3	398.6	43.15	0.65
Hegyi$_5$	−148.5	307.1	48.07	0.43	−194.7	399.4	42.91	0.65
Hegyi$_{10}$	−146.4	302.9	49.13	0.42	−191.8	393.7	44.56	0.64
P. pinea								
N$_5$	−308.9	627.9	24.03	0.33	−282.7	575.5	28.65	0.68
N$_{10}$	−310.8	631.7	22.99	0.33	−285.4	580.7	27.27	0.69
BAL$_5$	−319.6	649.3	17.98	0.35	−297.9	605.7	20.32	0.72
BAL$_{10}$	−300.9	611.7	28.3	0.32	−278.3	566.5	30.94	0.67
BALmod$_5$	−324.9	659.8	14.39	0.35	−304.3	618.5	16.3	0.74
BALmod$_{10}$	−324.4	658.7	15.16	0.35	−303.7	617.3	16.87	0.73
ISD$_5$	**−99**	**208.1**	**20.68**	**0.31**	−94.9	199.9	20.15	0.67
ISD$_{10}$	−219.5	449.1	26.67	0.30	−208.6	427.3	28.33	0.67
CE$_5$	−312.6	635.1	22.04	0.34	−285.7	581.3	27.11	0.69
CE$_{10}$	−312.1	634.3	22.28	0.34	−285.2	580.5	27.33	0.69
Hegyi$_5$	−323.7	657.3	15.59	0.35	−301.8	613.7	17.97	0.73
Hegyi$_{10}$	−321.6	653.1	16.84	0.35	−298.6	607.2	19.9	0.72

Table 4
Results of the fitted IPPM models for *P. pinaster* and *P. pinea* saplings. $Z(x,y)$ is the spatial covariate included in the model to estimate λ, the intensity of the point process model. $\lambda_Z(x,y)$ is the intensity of the IPPM model, KS *p*-val is the probability-value of the Kolmogorov–Smirnov test to check the validity of the model and AIC is the Akaike Information Criterion of the fitted model. The AIC of the most accurate model is in bold.

$Z(x,y)$	Plot	*P. pinaster*			*P. pinea*		
		$\lambda_Z(x,y)$	KS *p*-val.	AIC	$\lambda_Z(x,y)$	KS *p*-val.	AIC
DBH	1	exp(−3.99 to 0.61(x,y))	0.0143	1660	Not existing model	0.8802	2607
	2	Not existing model	0.1127	1174	exp(−2.22 + 0.15(x,y))	0.000	7288
h	1	exp(−4.03 to 0.45(x,y))	0.0996	1670	Not existing model	0.2782	2609
	2	exp(−5.09 + 0.96(x,y))	0.0833	1160	exp(−2.20 + 0.11(x,y))	0.000	7293
Growth	1	Not existing model	0.3687	1664	exp(−3.55 to 0.01(x,y))	0.06242	2609
	2	exp(−4.77 to 0.81(x,y))	0.0089	1186	exp(−2.19 to 0.19(x,y))	0.000	7285
Density of adult trees	1	exp(−5.31 + 58.6(x,y))	0.0846	**1643**	Not existing model	0.452	2608
	2	exp(−6.21 + 44.4(x,y))	0.0067	**1104**	exp(−2.08 to 2.53(x,y))	0.000	7298
Density of conspecific adult trees	1	Not existing model	0.6918	1677	Not existing model	0.3458	2574
	2	Not existing model	0.1397	1104	exp(−2.44 + 16.7(x,y))	0.000	7258
Density of heterospecific adult trees	1	Not existing model	0.7366	1543	exp(−3.28 to 29.2(x,y))	0.08871	**2601**
	2	Not existing model	0.1397	1104	exp(−1.49 to 90.2(x,y))	0.000	**6998**
Saplings of heterospecific individuals	1	Not existing model	0.7366	1543	Not existing model	0.5407	2593
	2	exp(−6.17 + 85.94(x,y))	0.0127	1036	exp(−1.9718.62(x,y))	0.000	7249
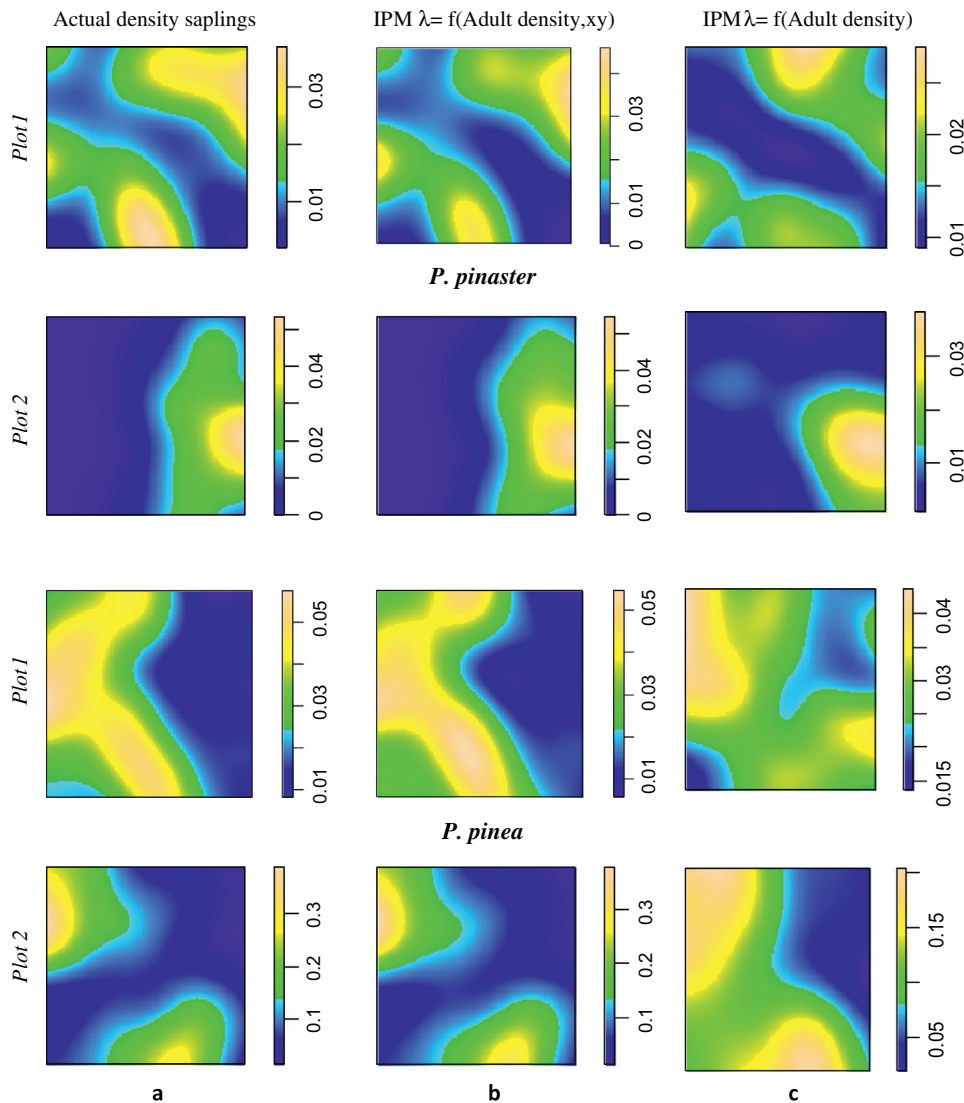
Fig. 2. Results of the IPPM fitted models for the distribution of *P. pinaster* (upper) and *P. pinea* (lower) saplings in plots 1 and 2 (a) actual distribution of sapling density, (b) a realization of the resultant IPPM including the spatial explanatory variable plus a function of the sapling coordinates (x,y) in λ estimation and (c) a realization of the resultant IPPM including the spatial explanatory variable in λ estimation. The explanatory variables were density of adult trees and density of heterospecific adult trees for *P. pinaster* and *P. pinea* respectively.

model provided a good estimation of sapling density. However, the inclusion of the spatial variation along with the spatial covariate in λ estimation resulted in greater accuracy and explanatory capacity of the models (Fig. 2b, Table 4). Hence, the inclusion of second order variation in sapling distribution improves the explanatory capacity of the model to describe sapling density in the plots.

In the case of *P. pinea*, an existing IPPM was obtained with a λ that included the spatial density of heterospecific adult trees only as an explanatory spatial variable. Once again, the models in both plots were similar (Table 4). The inclusion of the spatial variation along with the spatial covariate in λ estimation resulted in more accurate and explanatory models (Fig. 2, Table 4). For *P. pinea*, the spatial density of saplings depended not only on the position of adult trees but also on the species, unlike the distribution of *P. pinaster* saplings. The fitted models revealed that *P. pinea* saplings were distributed such that they avoid proximity to adult *P. pinaster* individuals, hence *P. pinea* saplings may be more likely to form clusters of conspecific individuals or mixed clusters rather than clusters of heterospecific individuals.

4. Discussion

Our study reveals that coexistence in the studied Mediterranean mixed pine forests is the result not only of silvicultural management but also of the interaction between similar spatial strategies and trade-offs between competition and facilitation, which change over the lifespan of the trees: sapling distribution was found to be positively related with that of adult trees, reflecting that facilitation is the driving process at that stage, whereas we found repulsion between individuals during the adult stage, when competition is the main factor influencing distribution. Competition tolerance differed between species, and was also found to be neighbor-species-dependent. Furthermore, a mixture of species is desirable in terms of productivity, in order to reduce competition. Mixed stands appear to be more efficient in terms of growth than pure stands. However, our results indicate that a change from a mixed stand to a pure *P. pinea* stand has been occurring naturally in recent decades.

4.1. Spatial arrangement and competition patterns of adult trees

The results from the spatial analyses revealed that the trees arise in mixed clusters of *P. pinaster* and *P. pinea* individuals, indicating a similar spatial strategy in both species. Furthermore, the clumps themselves also displayed a clustered pattern. This complex clustered distribution has been also reported in other studies in tropical ecosystems (Ledo et al., 2012; Wiegand et al., 2007) and has been attributed to the effect of two different overlapping mechanisms underlying primary and secondary dispersal (Wiegand et al., 2007). However, competition between trees within clusters was evident; with diameter size reflecting spatial repulsion, as expressed by the $K_{mm}(d)$ (Appendix 1). We found that *P. pinea* is capable of tolerating higher levels of competition than *P. pinaster*, as reflected by the competition indices (Table 2); *P. pinea* being surrounded by a greater number of individuals. Tree growth in both *P. pinaster* and *P. pinea* is more influenced (limited) by *P. pinea* neighbors (Fig. 2). This finding reflects differences in terms of tree response to the nature of conspecifics, indicating neighbor-asymmetric competition. This may indicate that *P. pinea* offers a greater competition value, perhaps due to its morphology [as previously reported for temperate and tropical forests (Coates et al., 2009; Harja et al., 2012)] and/or greater suitability to the region. Currently, drought is the main problem in the area (Gordo et al., 2012), and the roots of *P. pinea* may be capable of reaching

the deeper, humid regions of the soil which *P. pinaster* is not able to reach.

In the present study, in which we calculated competition tree per tree instead of per plot, the most explanatory competition index for both pine species was the Reineke ISD index, considering a 5 m radius around each tree. This short distance indicates tree to tree competition. This index considered both the number of trees and the DBH of the trees in a given radius around each tree. According to our results, this combination provides the most explanatory competition value in the growth models. For both *P. pinaster* and *P. pinea*, the use of distance-independent indices resulted in a more accurate growth model than when distance-dependent indices are used. The growth models revealed that *P. pinea* tolerates competition better in mixed than in pure clusters, so mixed stands may be preferable in terms of competition balance and increased productivity, as long as competition remains below certain levels.

4.2. Spatial distribution of saplings

Saplings of both species were spatially associated with adult individuals, as confirmed by the fitted IPPM models (Table 4), indicating that the aforementioned stand clumps are composed of both adult trees and saplings. It is known that both species require some degree of shelter to develop after recruitment as the extreme temperatures reached on bare soil can cause seedling death (Rodríguez-García et al., 2011; Barbeito et al., 2008). Hence, 'nursery conditions' are necessary if seedling mortality is to be avoided and seedlings are to develop in the studied Mediterranean stand (Castro et al., 2004). The protection offered by tree crowns is a necessary factor for seedling development, as reported by Rodríguez-García et al. (2011) for *P. pinaster* seedling recruitment and by Calama et al. (2012) and Manso et al. (2012) for *P. pinea* seedling recruitment in pure pine stands. However, in the present study, an important difference in effective recruitment niche preferences between the species was identified through the IPPM analyses. We assumed that the spatial pattern of saplings is limited by and related to the initial spatial distribution of seedlings following the effective recruitment process. Hence, the spatial pattern of saplings might be partially explained by the dispersion strategy of the species. *P. pinaster* occurs in close proximity to adult individuals, regardless of the species (Table 4, Fig. 2). *P. pinaster* is mainly wind dispersed, so the seed shadow tends to display a uniform spatial distribution (Del Peso et al., 2012), with the possibility of becoming established under *P. pinea* or *P. pinaster* crowns. However, *P. pinea* is not found under heterospecific trees (Table 4, Fig. 2). Furthermore, the position of *P. pinea* saplings was better explained when the square coordinates of tree position were included in the analysis (Fig. 2). The fact that in the models the coordinates are squared indicates the existence of secondary dispersal (Wiegand et al., 2007). Hence, what is more likely to be occurring in the case of *P. pinea* is that some saplings found around the parent trees are those derived from seedlings that were gravitationally dispersed, whereas other seedlings derived from secondary dispersal are spread throughout the plot, although these latter seedlings avoid proximity to *P. pinaster*. This also indicates greater effectiveness of secondary dispersal in the case of *P. pinea* compared to *P. pinaster*. As regards adult trees, *P. pinea* is a facilitation agent for saplings of both species, whereas *P. pinaster* only facilitates conspecific individuals (Table 4).

4.3. Implications of the results for species coexistence and stand maintenance

Competition was the main factor affecting adult tree growth (Fig. 2). However, the most suitable areas for regeneration are

those areas occupied by the clumps of trees, where saplings and seedlings can survive and develop thanks to the protection provided by the adults. A similar shift from facilitation in the early stages to competition in the adult stages has also been observed between closely related shrub taxa in arid ecosystems (García-Cervigón et al., 2013; Valiente-Banuet and Verdú, 2008). This facilitation in the early stages of tree development in the arid Mediterranean ecosystem is also in accordance with the stress gradient hypothesis (Bertness and Callaway, 1994).

In the studied stand, which can be considered a xeric site as a consequence of low precipitation and sandy soil (causing more severe soil drought), there is an area of coexistence of *P. pinea* and *P. pinaster* that has been favoured by silvicultural management. However, under different scenarios and in the absence of human intervention, it is likely that either *P. pinaster* or *P. pinea* would recruit and develop more effectively than the other species, so that the stand would be dominated by the more successful of the two species to the detriment of the mixed composition. Our analysis revealed that *P. pinea* is increasing its density, because the saplings of *P. pinea* are far more abundant than the saplings of *P. pinaster*. *P. pinea* tolerates a greater level of competition (Table 2) and due to its gravitational dispersion method often forms dense stands (Fig. 1), which may become impenetrable to *P. pinaster*.

Moreover, because of their greater mass, both the seeds and seedlings of *P. pinea* can be better adapted to survive the severe drought periods likely to occur in the area due to climate change (Castro et al., 2004). The adaptive advantage of *P. pinea* in the context of climate change (Benito-Garzón et al., 2008) along with its greater tolerance to competition may lead to a change in species dominance in the areas where the species currently coexist. *P. pinaster*, however, has a seed which is more capable of colonizing new areas and can 'move' further in order to survive in the region.

Human intervention, through management, can play an essential role in tipping this balance of coexistence. Both species are adapted to Mediterranean climatic conditions (Benito-Garzón et al., 2008); although human intervention is a key factor in traditionally managed pine stands. Moreover, in this case such intervention can be used to address the differences in ecological preferences and the possible dominance of one species over the other so that the current species coexistence is maintained, particularly given that both *P. pinea* and *P. pinaster* are important species with regard to the traditional economy of the area (Gordo et al., 2012).

5. Conclusions

P. pinaster and *P. pinea* coexist in mixed stands with a similar spatial arrangement. The species occur in mixed clusters, which, according to our models, optimize production, since competition between conspecific neighboring adult trees is greater than between heterospecific neighbors.

To the best of our knowledge, our study is the first to demonstrate the importance of facilitation (by tree crowns) in the early stages for tree species coexistence in Mediterranean environments. Furthermore, a shift from facilitation in the sapling stage to competition in the adult stage occurs, so a trade-off between facilitation and competition are essential to tree coexistence. Species mixture may be desirable in terms of increasing and diversifying productivity although under current conditions, *P. pinea* may dominate the stand in the future because its recruitment is more abundant, and tends to form clusters which may be impenetrable to *P. pinaster*. Besides, *P. pinea* tolerates greater competition in the adult stage from other *P. pinea* trees, contrary to *P. pinaster*. This may be due to the deeper root system, capable of reaching more water. Hence, adequate silvicultural management strategies need to be enforced to maintain the mixed stands, which optimize production as well as offering other economic advantages. Otherwise, if the current conditions continue, future stands may be dominated by *P. pinea*.

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.2014.02.038.

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