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Is spatial structure the key to promote plant diversity in Mediterranean forest plantations?

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Abstract

Mediterranean forest plantations are currently under an intense debate related to their ecological function, sustainability and future performance. In several Mediterranean countries, efforts are directed to convert pine plantations into mixed and more diverse forests. This research aims to evaluate the effect of the spatial configuration of pine plantations on regeneration and plant diversity in order to facilitate plantation management towards more diversified stands. Spatial characteristics of plantations (proximity to different vegetation types, fragmentation and internal patch structure) were related to abundance of seedlings of an ecologically important broadleaved species, Holm Oak (*Quercus ilex* L.), and the Shannon diversity index of the community. *Q. ilex* seedling abundance and plant diversity in pine plantation patches are favoured by the proximity to oak patches located uphill. Fragmentation affected only plant diversity, with smaller patches having more diversity. The internal structure of the pine patch influenced both regeneration of *Q. ilex* and diversity. Pine patches with lower pine tree density were characterized by higher diversity and less *Q. ilex* regeneration confirming that internal structure affects species differently. From a management perspective, the process of conversion of Mediterranean pine plantations to mixed oak–pine forests could be facilitated by (1) having the seed source uphill from the plantation, (2) increasing the fragmentation of plantations and (3) promoting the internal heterogeneity of plantations to create a diverse range of light environments matching the different requirements of species.

Zusammenfassung

Die ökologische Funktion, die Nachhaltigkeit und die Zukunft der Plantagenwirtschaft im Mittelmeerraum werden gegenwärtig heftig diskutiert. In verschiedenen Ländern des Mittelmeerraumes sollen Kiefernplantagen in arten- und struktureichere Mischbestände umgebaut werden. Ziel dieser Forschungsarbeit ist es, den Einfluss der räumlichen Beschaffenheit von Kiefernplantagen auf Verjüngung und Pflanzendiversität einzuschätzen, damit der Umbau zu vielfältigeren Beständen erleichtert werden kann. Die räumlichen Eigenschaften der Bestände (Nähe zu anderen Vegetationstypen, Fragmentierung und Struktur) korrelieren mit der Häufigkeit von ökologisch wichtigen Eichensämlingen, Steineiche (*Quercus ilex*), und dem Shannon Diversitätsindex der Gemeinschaft. Die Häufigkeit von *Q. ilex*-Sämlingen und die Pflanzenvielfalt der Kiefernflächen werden durch

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die Nähe zu Eichenflächen in höher gelegenen Lagen positiv beeinflusst. Die Fragmentierung der Bestände beeinflusst lediglich die Pflanzenvielfalt, wobei kleinere Flächen vielfältiger sind. Die Struktur der Bestände beeinflusst sowohl die Verjüngung von *Q. ilex* als auch die Pflanzenvielfalt. Weniger dichte Teile der Kiefernbestände werden durch eine höhere Vielfalt und weniger *Q. ilex* Verjüngung charakterisiert. Dies bestätigt, dass Pflanzenarten unterschiedlich auf heterogene Mikrohabitate reagieren. Der Umbau von mediterranen Kiefernplantagen zu Eichen-Kiefern-Mischbeständen kann erleichtert werden wenn (1) sich Samenbestände in höheren Lagen als der umzubauende Bestand befinden, (2) Plantagen auf der Landschaftsebene stärker fragmentiert werden und (3) die interne Heterogenität der Bestände verbessert wird um eine breite Streuung der Lichtverhältnisse zu schaffen, die den unterschiedlichen Anforderungen verschiedener Arten gerecht wird.

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Keywords: Fragmentation; Shape; Landscape ecology; Context; Geometry; Spatial configuration; Distance; Dispersal

Introduction

Forest plantations cover more than 9 million ha in the Mediterranean basin, representing ca. 12% of the total forest cover (FAO 2006). A large extent of these plantations is the result of reforestation programs, carried out since the 19th century (Pausas et al. 2004). Nowadays the state of Mediterranean plantations is intensively debated because of their ecological function and sustainability (Pausas et al. 2004; Gómez-Aparicio, Zavala, Bonet, & Zamora 2009). In degraded areas, pines (pioneer species) were mainly used for plantations, assuming that they would facilitate succession towards more late-successional species such as oaks (Pausas et al. 2004). Pine plantations might provide adequate microclimatic conditions for regeneration of late successional species when environmental barriers block tree regeneration (Lookingbill & Zavala 2000; Brockerhoff, Jactel, Parrotta, Quine, & Sayer 2008). Nevertheless, many pine plantations have not evolved in the desired direction forming nowadays a low resilient ecosystem with limited species richness and little oak regeneration in the understory (Andrés & Ojeda 2002; Maestre & Cortina 2004). Thus, current management trends are based on the promotion of diversified stands (e.g. mixed stands of pine and oak species), which will meet not only the original protective and productive functions of pine plantations but also other factors such as biodiversity or recreation (Brockerhoff et al. 2008).

Understanding the patterns of plant diversity and oak regeneration in Mediterranean plantations is vital to promote the transition to more diversified stands. Plant diversity and oak regeneration in plantations will depend on a combination of several factors such as abiotic conditions, landscape structure and internal vegetation structure (Harrington & Edwards 1999; Utsugi et al. 2006; Gómez-Aparicio et al. 2009). First, abiotic conditions shape the response of species that could appear in pine plantations. For instance, specific hard climatic conditions at high altitude hamper the occurrence of oak species which are adapted to milder conditions (Gómez-Aparicio et al. 2009).

Second, considering landscape structure two aspects might be relevant, the vegetation surrounding the plantation (vegetation context) and fragmentation. The vegetation context will determine which species could arrive by dispersion

(Hewitt & Kellman 2002; Gómez-Aparicio et al. 2009). The effect of vegetation context on seed arrival may vary with the type of surrounding vegetation and the topographic position in the landscape. Some studies have found that the biodiversity of lower quality forests (i.e. low species and structure diversity) decreases with the distance to species-rich forests (Dzwonko & Loster 1992; Hewitt & Kellman 2002) although we are not aware of specific studies in Mediterranean plantations assessing the relative importance of different adjacent vegetation types. Considering topography in the vegetation context might be complex and has been seldom studied. Mountain areas are anisotropic surfaces where the downhill dispersal of propagules might be easier due to the effect of gravity (Bonet 2003; Li & Zhang 2003; Ohsawa, Tsuda, Saito, Sawada, & Ide 2007).

Fragmentation of plantation patches (i.e. area or shape complexity) might affect the rate of propagules arrival and the environmental conditions (mainly light and water) in the patch (Hill & Curran 2003). Most studies in this field have focused on diversity of remnant tropical forests patches. Under those conditions, patches with smaller area will have lower species richness due to the lower population capacity and the higher edge effects (Hill & Curran 2003; Galanes & Thomlinson 2009). Due to edge effects, these patches will have higher ratio between edge and interior habitat increasing the amount of pioneer species against the more diversified mixture of late-successional species of the interior (Laurance 1991). However, the opposite might occur in plantations where the increasing edge habitat might facilitate the establishment of other species (Utsugi et al. 2006).

Third, plant germination and establishment might be strongly linked to the internal structure of plantation patches in terms of tree density (Utsugi et al. 2006; Gómez-Aparicio et al. 2009). Plantations provide a matrix of different light microhabitats where plants can develop (Gómez, Valladares, & Puerta-Piñero 2004). In general, higher rates of species richness and seedling abundance will occur at medium or low tree density where light availability meets the needs of different species (Gómez-Aparicio et al. 2009).

As a first approximation in a previous research in the same study area, we evaluated differences in environmental gradients (climate, distance to oak vegetation and stand density) on plant regeneration and diversity between pine plantation

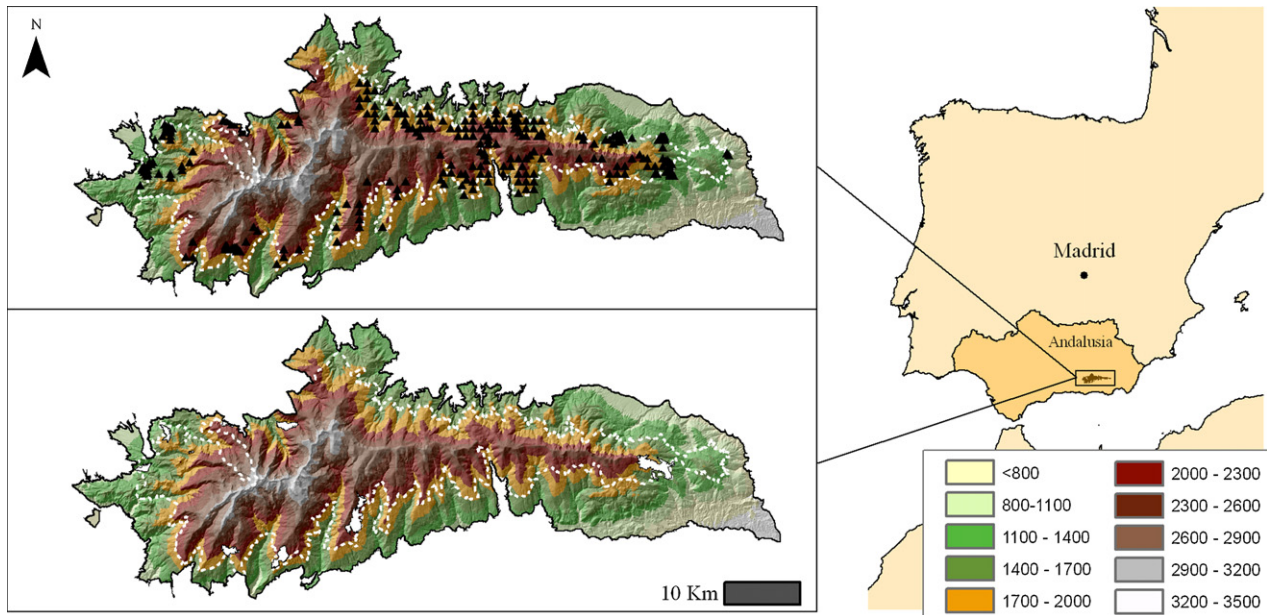


Fig. 1. Map of the study area (Sierra Nevada National Park, Southeast Spain) and the dataset used in the analysis. The white dotted line indicates the limit of the Sierra Nevada National Park and the continuous line indicates the limit of the Natural Park. Black triangles indicate the forest inventory plots used in the vegetation context and internal structure analysis ($n = 275$; upper map). Patches used for fragmentation analysis are highlighted in white ($n = 10$; lower map).

and natural oak stands (Gómez-Aparicio et al. 2009). Here, we focused on a meso-scale assessment of the spatial configuration of pine plantations at different spatial scales using novel methodologies and considering new factors (i.e. fragmentation). Specifically, we asked how natural regeneration and plant diversity within pine plantation patches are related at the landscape scale to the vegetation context of plantation patches (proximity to seed sources as dependent on surrounding vegetation types and their topographic position) and the fragmentation of plantation patches (area, perimeter and patch shape complexity). And how they are related at patch scale to the internal structure (tree density) of plantation patches. We predict that plantation patches closer to species-rich patches (e.g. oak or riparian vegetation), with higher fragmentation (smaller area and higher shape complexity) and more heterogeneous internal structure in terms of light availability (lower tree density) will show higher rates of oak regeneration and plant diversity. The answers to these questions are critical for the management of these highly anthropogenic systems because the spatial structure can be easily modified by forest managers.

Methodology

Study site

The study was conducted in the Sierra Nevada National Park (Southeast Spain), a mountain region with an altitudinal range between 860 m and 3482 m a.s.l. (Fig. 1). It has an extension of more than 2000 km². Annual average tem-

perature decreases from 12 to 16 °C below 1500 m to 0 °C above 3000 m. The average annual precipitation oscillates from 250 mm in the lowest and eastern part, to more than 700 mm on the highest peaks.

Forest cover in the Sierra Nevada National Park is dominated by pine species (79%). Most of them are plantations from the period 1960–1980 covering approximately 18,000 ha. *Pinus halepensis* Mill. is mainly found in low-altitude plantations (<1300 m) whilst *Pinus nigra* Arnold. subsp. *salzmannii* (Dunal) Franco and *Pinus sylvestris* L. grow at higher altitudes (>1900 m). At intermediate altitudes the three species are combined with *Pinus pinaster* Ait. Autochthonous *P. sylvestris* var. *nevadensis* forests can also be found in small patches at high altitudes with a characteristic low tree cover. Oak stands are mainly situated at lower altitudes than pine plantations. They are dominated by *Quercus ilex* subsp. *ballota* (Desf.) Samp. and *Quercus pyrenaica* Willd.

Dataset

A simplified version of the forest map of Andalusia 1:10,000 (CMA 2001) was used as the landscape mosaic to define different vegetation patches, identify pine plantation areas and calculate vegetation context and fragmentation variables (Supplementary data, Fig. 1). The different vegetation classes used were selected according to their possible contribution to regeneration and plant diversity in pine plantations. The vegetation classes were: (1) pine plantation (>50% tree cover and >75% pine), (2) natural and semi-natural pine (3) oak and broadleaved species (>5% tree cover and oak

presence), (4) shrublands (<5% tree cover and >20% shrub cover), (5) riparian vegetation and (6) agricultural fields. Alpine shrubland (>1800 m a.s.l.), with species mainly not adapted to forest conditions, was not selected to avoid confusion with species-rich shrubland areas of low-mid altitude.

Oak regeneration and plant diversity variables: Regeneration and plant diversity variables were obtained from the forest inventory of Sierra Nevada National Park (SIN-FONEVADA) collected during 2004 and 2005: 275 Forest inventory plots within pine plantation patches were selected according to the simplified vegetation map (Fig. 1). Plots without pine canopy and influence of special elements such as paths or streams were omitted. Plots in small gaps within pine plantation patches were accepted. Plot size ranged from 300 to 400 m². Species identity was recorded of every live tree with a diameter of at least 7.5 cm (DBH). Two additional subplots were established within each larger plot: a 5-m radius plot to measure the number of seedlings (DBH < 2.5 cm and height < 1.3 m) of tree species, and a 10-m radius plot to measure the species composition and abundance. Regeneration was measured as seedling abundance in the 5-m radius subplot. The oak species considered in the analysis was *Q. ilex*. Other species were not taken into account due to their low seedling abundance in the inventory. Oak saplings were not considered, since they could have been established before the establishment of the plantation. Plant diversity was measured using the Shannon diversity index (H'):

$$H' = -\sum_{i=1}^S (p_i \ln p_i) \quad (1)$$

where p_i is the proportion of accumulated percent cover of each species.

It was calculated for the total of species and considering separately herbaceous species, fleshy-fruited woody species and dry-fruited woody species from the 10-m radius subplot (Supplementary data, Tables 1–3 for species list). The division among woody species addresses the differences in dispersal syndrome: fleshy-fruited woody species usually have endozoochorous syndromes whilst the rest of species can have other dispersal syndromes such as exozoochory or anemochory. This distinction was not made for herbaceous species because most of them (>95%) have dry fruits and abiotic dispersal.

Spatial structure variables: The vegetation context of plantation plots was analyzed as the distance between the central point of the inventory plot and the different vegetation classes considered using ArcGIS 9.2 (ESRI Inc., Redlands, USA). Three different algorithms were used for each vegetation class: Euclidean distance and weighted distance to penalize downhill or uphill movements. The weighted distance was applied to account for topography and it was calculated by multiplying the Euclidean distance by a slope factor that changed according to the steepness and the direction of the

slope in steps of 10 m:

$$\text{Uphillfactor} = 1 - A \times \text{slope} \quad (2)$$

$$\text{Downhillfactor} = 1 + A \times \text{slope} \quad (3)$$

where the slope is in degrees (−90 to 90) and A is 0.0111 to perform a linear function with range −90 to 90 that equals one when the terrain is flat (slope = 0).

The uphill function (Eq. (2)) favours uphill movements giving lower slope factor (reduce Euclidean distance) at positive slope. In the opposite way, the downhill function (Eq. (3)) favours downhill movement. Slope information was provided by the Digital Elevation Model (DEM) of Andalusia (ICA 2005) with a spatial resolution of 10 m. This method did not address distances of real dispersal events and it is possible that real dispersal distances were underestimated. Fragmentation of pine plantation patches was quantified as area, perimeter and two shape complexity indices, shape index (Hill & Curran 2003) and fractal dimension (Turner & Gardner 1991) using ArcGIS 9.2. The shape index equals the perimeter of the patch (m) divided by the minimum perimeter (m) possible of a circle of the corresponding patch area. Fractal dimension equals 2 times the logarithm of patch perimeter (m) divided by the logarithm of patch area (m²). Preliminary analyses showed significant and strong relationships between area and perimeter and between both shape complexity indices (Supplementary data, Table 4). Thus, only area and shape index were selected for further analysis due to their simplicity and extensive use (Hill & Curran 2003). The internal structure of plantation plots was quantified as tree density per ha from the forest inventory.

Abiotic variables: Two abiotic variables, altitude and annual radiation, were included in the analyses to control climatic differences in the relationship between the spatial configuration and regeneration and plant diversity (Gómez-Aparicio et al. 2009). Soil variability was not included in the research as most of the study area is in limestone.

Data analyses

Vegetation context and internal structure: The effect of vegetation context and internal structure on plant diversity and regeneration was analyzed at the plot level ($n = 275$, Supplementary data, Table 5). Vegetation context variables for each inventory plot were related to regeneration and plant diversity variables using the Pearson correlation coefficient. Stepwise Generalized Linear Models (GLMs) were used to control for climate differences and to determine the variables that explain most variability. GLMs were built for each subset of factors (i.e. abiotic, context and internal structure) and including all factors. Within context variables, only the best algorithm for each vegetation class from correlation analysis was selected, thus avoiding collinearity problems. The error terms for the diversity data were modelled using a normal distribution, whereas the error terms for the regeneration data were modelled using a Poisson distribution which is typi-

Table 1. Pearson correlation coefficients between regeneration (log seedling abundance of *Q. ilex*) and plant diversity (Shannon diversity index for total species, herbaceous species, dry-fruited and fleshy-fruited woody species) and vegetation context variables (distances calculated from pine plantation plots to different vegetation classes), $n = 275$. Riparian distance was square root transformed and all other context variables were double square root transformed.

	Plant diversity				Regeneration
	H' _{total species}	H' _{herbaceous}	H' _{woody dry}	H' _{woody fleshy}	Seedlings _{Qilex}
<i>Euclidean distance</i>					
Oak	-0.21**	-0.21***	-0.28***	-0.12*	-0.33***
Shrubland	-0.17**	-0.09	-0.18**	-0.27***	-0.10
Riparian	-0.18**	0.05	-0.21***	-0.20**	-0.00
Fields	-0.03	-0.1	-0.1	0.26***	-0.07
<i>Weighted distance downhill</i>					
Oak	-0.22***	-0.21***	-0.29***	-0.14*	-0.33***
Shrubland	-0.18**	-0.12	-0.21***	-0.27***	-0.13*
Riparian	-0.18**	0.04	-0.22***	-0.20**	-0.00
Fields	-0.05	-0.12	-0.11	0.23**	-0.09
<i>Weighted distance uphill</i>					
Oak	-0.20**	-0.16**	-0.27***	-0.10	-0.32***
Shrubland	-0.15*	-0.05	-0.13*	-0.26***	-0.07
Riparian	-0.18**	0.1	-0.22**	-0.20**	0.01
Fields	-0.01	-0.06	-0.07	0.27***	-0.06

Significant correlations are given in bold: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

cally used for count data. Models were selected by Akaike's Information Criterion; Δ AIC (Akaike 1992).

Fragmentation: The effect of fragmentation was analyzed at the patch level ($n = 10$, Supplementary data, Table 6). The continuity of pine areas in the study site makes it difficult to delimit isolated patches in order to study the patch fragmentation effect (see Supplementary data, Fig. 1). Therefore, only clearly isolated patches were selected. The selection criteria were clear isolation to delimit edges and at least one inventory plot within the patch. The selected patches cover the whole range of the study area (Fig. 1). Regeneration, plant diversity and abiotic variables were quantified as the average of the values of all inventory plots within each patch. Fragmentation variables were related to regeneration and plant diversity variables using the Spearman correlation coefficients due to the absence of normality. Stepwise GLMs were used to control for climate differences. All statistical analyses were performed with R v 2.9.2 (R Development Core Team, Vienna, Austria).

Results

Vegetation context

Plant diversity: Plant diversity of all species and woody species declined significantly with increasing distance to oak vegetation, shrublands and riparian vegetation (Table 1). The diversity index for fleshy-fruited woody species was positively correlated to distance to agriculture fields. Diversity of herbaceous species was negatively correlated to the distance to oak vegetation (Tables 1 and 2). Regarding the

topographic position, the algorithm favouring downhill dispersion showed slightly stronger correlation strength than the others (weighted downhill > Euclidean > weighted uphill) (Table 1, Supplementary data, Fig. 2), although the differences were not significant. All diversity indices except the index for herbaceous species followed this pattern.

Regeneration: There were virtually no *Q. ilex* found at more than 1000 m from oak vegetation. However, a high proportion (72%) of inventory plots with *Q. ilex* regeneration were found at less than 250 m from oak vegetation and almost all at less than 500 m (90%). The seedling abundance of *Q. ilex* was strongly negatively related to the distance to oak patches (Tables 1 and 2). Abundance of *Q. ilex* seedlings also showed similar pattern of differences among distance algorithms to plant diversity indices (Euclidean = weighted downhill > weighted uphill) (Table 1). However, the differences were not significant.

Fragmentation

Plant diversity: Correlation analysis did not show any significant relationship between plant diversity indices and fragmentation variables. However, regression analyses showed significant relationships with fragmentation variables once climate was controlled (Table 3). Area had a negative effect on plant diversity of all species whilst shape index had a positive effect. This trend was also found for plant diversity of woody species but not for herbaceous species.

Regeneration: Abundance of *Q. ilex* seedlings did not show significant relations with any of the fragmentation variables considered (Table 3).

Table 2. Comparison of models of plant diversity (Shannon diversity index for total species, herbaceous species, dry-fruited and fleshy-fruited woody species) and oak regeneration (seedling abundance of *Q. ilex*) related to vegetation context (distance to vegetation patches), internal structure (tree density) and abiotic variables (altitude and annual radiation) ($n = 275$).

	Model	AIC	Δ AIC	R^2	Independent variables included
<i>Plant diversity</i>					
$H'_{\text{total species}}$	Full	380.00	0.00	0.38	–ALT –DEN
	Internal st.	397.64	17.64	0.34	–DEN
	Abiotic	476.00	96.00	0.12	–ALT
	Context	494.21	114.21	0.07	–OAK –RIPA
	Null	510.10	130.10		
$H'_{\text{herbaceous}}$	Full	461.63	0.00	0.09	–ALT +RAD –OAK –DEN +RIPA
	Context	469.50	7.87	0.04	–OAK
	Abiotic	471.51	9.88	0.04	–ALT +RAD
	Internal st.	472.55	10.92	0.03	–DEN
	Null	479.92	18.29		
$H'_{\text{woody fleshy}}$	Full	312.58	0.00	0.25	–RAD –SHR +CROP –DEN
	Context	329.73	14.78	0.20	–SHR +CROP –RIPA
	Abiotic	345.62	30.67	0.14	–RAD
	Internal st.	375.80	60.85	0.04	–DEN
	Null	385.74	70.79		
$H'_{\text{woody dry}}$	Full	216.01	0.00	0.34	–ALT –DEN
	Abiotic	259.23	43.22	0.24	–ALT
	Internal st.	270.06	54.05	0.20	–DEN
	Context	300.50	84.49	0.12	–OAK –RIPA
	Null	330.24	114.23		
<i>Regeneration</i>					
Seedlings Qil	Full	5551.30	0.00	0.19	–ALT +RAD –OAK +DEN
	Context	5996.80	445.50	0.12	–OAK
	Abiotic	6107.50	556.20	0.10	–ALT +RAD
	Internal st.	6666.90	1115.60	0.01	+DEN

Note: Models are ranked from best to poorest fits. AIC (Akaike's Information Criteria) is calculated as: $AIC = -2 \log(Lq|data, model) + 2K$, being K the number of parameters in the model. Model fits are evaluated through ΔAIC ($AIC_i - AIC_{\text{min}}$) and $R^2 = 1 - \text{Residual Deviance}/\text{Null Deviance}$. Abbreviations of variables included in each model are: ALT, altitude; CROP, distance to crops; DEN, tree density; OAK, distance to oak; RAD, annual radiation; RIPA, distance to riparian vegetation; SHR, distance to shrubland. The sign +/- on the left of each variable indicates the positive/negative relationship with the dependent variable.

Internal structure

Plant diversity: Shannon diversity indices for all species and for the individual species groups were negatively related to tree density (Table 2). The best regression models for all indices (except for fleshy-fruited woody species) included always the internal structure component. However their explanatory strength changed depending on the groups of species considered (Table 2).

Regeneration: Abundance of *Q. ilex* seedlings was positively related to tree density but with very low explanatory strength (Table 2).

Discussion

Our results confirm that regeneration and plant diversity in pine plantations are influenced by the spatial configuration at different scales. Specifically, there is a greater influence at the landscape scale (vegetation context and fragmentation) than at the patch scale (internal structure) for oak regeneration,

whilst the opposite applies to overall plant diversity. Nevertheless, this effect is constrained by abiotic conditions, which vary largely in the mountainous study area (Gómez-Aparicio et al. 2009). The multiscale approach used has proven that processes at different scales influence the overall outcome expressed at the patch level (Turner, Gardner, & O'Neill 2001). However the response varied depending on the group of species and spatial variables considered.

Vegetation context (proximity to seed source)

For successful establishment, the propagules must arrive from vegetation patches surrounding pine plantations. Our results indicate that distance to these vegetation patches might determine the abundance and presence of other species than pine, which is in line with the theory that seed dispersal is inversely related to the distance to the seed source (Hewitt & Kellman 2002). Nevertheless, these variables were not able to explain a high variance of plant diversity or oak regenera-

Table 3. Best regression models explaining plant diversity variables (Shannon diversity index for total species, herbaceous, dry-fruited and fleshy-fruited woody species) and oak regeneration (seedling abundance of *Q. ilex*) by abiotic (ALT = altitude, RAD = annual radiation) and fragmentation variables (SI = Shape complexity index, AREA = patch area) ($n = 10$). Standardized coefficients are given for each variable in the model.

	$H'_{\text{total spp}}$	H'_{herb}	$H'_{\text{woody dry}}$	$H'_{\text{woody fleshy}}$	Seedlings _{Qilex}
Model	$F_{3,6} = 23.71^{***}$	$F_{2,7} = 1.54$	$F_{3,6} = 21.05^{**}$	$F_{3,6} = 12.93^{**}$	$F_{2,7} = 2.33$
R^2	0.92	0.31	0.91	0.86	0.40
ALT	-0.61**		-0.88***		-0.78
RAD				-0.49*	0.66
SI	0.96**	0.64	0.63*	0.86**	
AREA	-1.06***	-0.84	-0.52*	-0.98**	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

tion. Therefore, it might be possible that other similar factors such as the amount of non pine vegetation surrounding the plantation might better represent the propagule pressure into pine plantations.

Of all vegetation types considered, oak vegetation was the most influential. Oak vegetation has higher plant diversity than pine plantations, especially for herbaceous species (Gómez-Aparicio et al. 2009). Thus, smaller distances could increase the pool of species in the plantation and reduce the evenness of plantation communities. Distance to shrubland vegetation and riparian vegetation were positively related to diversity of all species and diversity of woody species. For shrubland, this relation might be the result of seed dispersal by frugivorous birds (Zamora, Hodar, Matías, & Mendoza 2010). The decline in diversity with distance to riparian vegetation might either indicate that diversity is higher when riparian seed sources are nearby, or that diversity is higher in areas close to mesic sites with higher water availability and deeper soils.

We also found some slight evidence that seed dispersal tends to come from species-rich patches situated at relatively higher altitude compared to the pine plantation plots. Although this mechanism has been poorly investigated, several studies have found that oak seeds tend to be dispersed downslope, because of the gravity effect (Ohsawa et al. 2007) or because of the energy saving behaviour of dispersal vectors (Li & Zhang 2003). Nevertheless, these studies were performed at smaller scale and in the case of Ohsawa et al. (2007) analyzing genetic links. Thus, to firmly confirm our findings it will be necessary to perform additional controlled experiments involving spatial genetic analyses or tracking the movement of dispersal agents.

Fragmentation (area and shape complexity)

The fragmentation of pine plantations increases plant diversity of woody species: the diversity increases with increasing shape complexity and decreasing patch size. Higher shape complexity might enhance interception of seeds or dispersal vectors due to the increase of contact area,

thus increasing recruitment within plantation patches (Hill & Curran 2003). Furthermore, some species might be also favoured by the increasing light conditions of patch edges (Matlack 1994; Utsugi et al. 2006). Therefore, if the edge becomes longer in relation to the patch area, there will be more suitable habitat for the establishment of these species. These results are partially in contrast with the findings for tropical forests where decreasing patch size leads to biodiversity loss (Hill & Curran 2003). However, shape complexity of tropical forest patches seems also to have a positive effect on biodiversity (Galanes & Thomlinson 2009), though the effect might depend on the group of species considered (Hill & Curran 2003). In contrast to tropical forests, plantations are rather homogeneous and artificial systems. Thus, fragmentation of plantations in terms of both patch area and shape complexity will increase habitat heterogeneity facilitating a spectrum of microhabitats suitable for a wide range of species.

On the other hand, *Q. ilex* regeneration was not significantly influenced by patch fragmentation which suggests that its effect is species-dependent. This could be explained by the European jay (*Garrulus glandarius* L.), the most important dispersal vector of *Q. ilex* (Bosema 1979), which could not be affected by the increase of contact area. Furthermore, oak seedlings might not be favoured by the increasing light availability in the patch edge which is in line with the negative relation to tree density.

Internal structure (tree density)

The internal vegetation structure expressed as tree density determines regeneration and plant diversity in different ways. Plant diversity was higher in plots with lower tree density, suggesting that higher light availability leads to more niches for different species. This result is in agreement with the extensive literature that stresses the positive relationship between light availability and species abundance in plantations (Utsugi et al. 2006; Gómez-Aparicio et al. 2009). In contrast, the abundance of *Q. ilex* seedlings was lower in plots with lower tree density. European jays prefer to cache

acorns close to specific habitat elements such as pine trees (Gómez 2003). This behaviour not only helps jays to find the acorns afterwards but also creates a characteristic pattern of oak recruitment which depends on an existing pine canopy. Thus, dense and homogeneous areas within pine plantation patches might be more suitable for dispersal by jays due to the continuity of pine cover. This dispersal behaviour allows tree seedlings to develop in the required shaded conditions, but it may reduce survival in the sapling stage, when higher light availability is required (Espelta, Riba, & Retana 1995).

Implications for management

Since 1990, 21% of the pine plantation area in the Sierra Nevada National Park has been treated to facilitate the conversion to more diversified stands. For future works, our results suggest that plant diversity in Mediterranean plantations can be enhanced by taking the abiotic constraints of the species into account (Gómez-Aparicio et al. 2009) and by silvicultural interventions that change the spatial structure of the forest. First, for pine plantations further than 500 m away from oak seed sources, active sowing or planting is needed to guarantee oak regeneration. To enhance dispersal success later on, these treatments could be applied mainly in the higher situated areas of the plantations to benefit from downhill dispersal events. Second, large and continuous plantation patches should be fragmented in order to increase landscape heterogeneity. Third, internal structure management must balance the need for light availability to increase plant diversity with the need for shade conditions to enhance oak recruitment. In areas where sufficient oak regeneration is already present in the seedling bank, it might be necessary to carry out thinning in order to enhance the diversity and improve oak growth in the sapling stage. Where regeneration is scarce, thinning could be done at different intensities within patches. In this way some areas will remain structurally homogeneous (with continuous canopy cover) to encourage oak dispersal, whereas other areas will have higher light availability leading to higher plant diversity.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2011.02.012.

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