

Running head: regeneration and diversity in plantations along gradients

**Are pine plantations valid tools for restoring Mediterranean forests? An assessment along gradients of climatic conditions, stand density and distance to seed sources**

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## 1 ABSTRACT

2 The ecological impacts of forest plantations are a focus of intense debate, from studies  
3 that consider plantations as “biological deserts” to studies showing positive effects on plant  
4 diversity and dynamics. This lack of consensus might be influenced by the scarcity of studies  
5 that examine how the ecological characteristics of plantations vary along abiotic and biotic  
6 gradients. Here we conducted a large-scale assessment of plant regeneration and diversity in  
7 plantations of southern Spain. Tree seedling and sapling density, plant species richness, and  
8 Shannon’s ( $H'$ ) diversity index were analysed in 442 pine plantation plots covering a wide  
9 gradient of climatic conditions, stand density, and distance to natural forests that act as seed  
10 sources.

11 Pronounced variation in regeneration and diversity was found in plantation understoreys  
12 along the gradients explored. Low-mid altitude plantations showed a diverse and abundant  
13 seedling bank dominated by *Quercus ilex*, whereas high-altitude plantations showed a virtually  
14 monospecific seeding bank of *Pinus sylvestris*. Regeneration was null in plantations with stand  
15 densities exceeding 1500 pines/ha. Moderate plantation densities (500-1000 pines/ha) promoted  
16 recruitment in comparison to low or null canopy cover, suggesting the existence of facilitative  
17 interactions. *Quercus ilex* recruitment diminished exponentially with distance to the nearest *Q.*  
18 *ilex* forest. Richness and  $H'$  index values showed a hump-shaped distribution along the  
19 altitudinal and radiation gradients, and decreased monotonically along the stand density gradient.

20 From a management perspective, different strategies will be necessary depending on  
21 where a plantation lies along the gradients explored. Active management will be required in  
22 high-density plantations with arrested succession and low diversity. Thinning could redirect  
23 plantations towards more natural densities where facilitation predominates. Passive management

1 might be recommended for low-moderate density plantations with active successional dynamics  
2 (e.g., towards oak or pine-oak forests at low-mid altitudes). Enrichment planting will be required  
3 to overcome seed limitation, especially in plantations far from natural forests. We conclude that  
4 plantations should be perceived as dynamic systems where successional trajectories and diversity  
5 levels are determined by abiotic constraints, complex balances of competitive and facilitative  
6 interactions, the spatial configuration of native seed sources, and species life-history traits.

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8 *Key words: competition; environmental gradients; facilitation; management strategy;*  
9 *Mediterranean forests; pine plantations; regeneration; seed dispersal; species diversity; stand*  
10 *density.*

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## INTRODUCTION

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Humans play a key role in shaping the structure and abundance of most ecosystems around the world (Sanderson et al. 2002, Haberl et al. 2007). The significance of the human footprint has been formally recognized in the term “emerging ecosystems”, defined as ecosystems where species occur in combinations and relative abundances that have not occurred previously within a given biome and that are the result of deliberate or inadvertent human action (*sensu* Hobbs et al. 2006). An example of this type of novel or emerging ecosystems are forest plantations (Chazdon 2008), usually characterized by higher stand density, lower tree diversity, and different specific composition than in natural forests (Hartley 2002, FAO 2005). The area covered by forest plantations has increased dramatically in recent decades, currently representing approximately 140 million ha worldwide (FAO 2005). Although only a 22% of this area has a primarily protective function (i.e., conservation of soil, water and biodiversity), the importance

1 of plantations in landscape management and restoration has increased recently, environmental  
2 protection being considered a legitimate objective even for productive plantations (Lamb 2005,  
3 Cummings and Reid 2008).

4         The ecological impacts of forest plantations is a focus of intense debate, from studies that  
5 consider plantations as “biological deserts” with deprived vegetation diversity and dynamics, to  
6 studies showing neutral or even positive effects on environmental conditions and biodiversity  
7 (Lugo 1997, Cannell 1999, Moore and Allen 1999, Kanowski et al. 2005, Stephens and Wagner  
8 2007). Thus, there is evidence that plantation forests can accelerate forest succession on  
9 previously deforested sites and abandoned agricultural areas where persistent ecological barriers  
10 to succession (e.g., extreme climatic conditions, competition with grasses) might otherwise  
11 preclude re-establishment of native species (Gardiner et al. 2004, Lamb et al. 2005, Brockerhoff  
12 et al. 2008). However, plantations have also been shown to strongly decrease resource levels in  
13 the understorey (i.e., light, soil water, and nutrients) negatively affecting diversity and  
14 performance of native plant species (Cavelier and Tobler 1998, van Wesenbeeck et al. 2003,  
15 Bellot et al. 2004, Maestre and Cortina 2004). This lack of consensus has relevant applied  
16 consequences, since it questions the value of plantations as restoration tools.

17         Discrepancies around the ecological consequences of forest plantations can arise, among  
18 other reasons, from the scarcity of studies that examine plantations along gradients of  
19 environmental conditions and stand characteristics. First, abiotic conditions (i.e., climatic  
20 characteristics, soil fertility) will influence the suitability of a plantation for natural regeneration  
21 and diversity recovery. For example, a few studies have shown that the suitability of pine  
22 plantations for woody species regeneration in Mediterranean areas is reduced in dry years and  
23 sites, presumably due to more intense competition for water (Maestre et al. 2004, Arrieta and

1 Suarez 2006). Secondly, the stand structure of the plantation will influence the establishment of  
2 native species through biotic interactions such as competition (Grace and Tilman 2003) and  
3 facilitation (Callaway 2007). In this sense, the sign and magnitude of overstorey-understorey  
4 interactions might change as a function of overstorey density (Thomas *et al.* 1999, Arévalo and  
5 Fernández-Palacios 2005, Paquette *et al.* 2006). However, the scarcity of studies that explore  
6 plantation effects along tree density gradients precludes identifying density thresholds that define  
7 the transition between negative and positive net effects on understorey vegetation. Finally, in  
8 fragmented landscapes, dispersal distances and the frequency of long-distance dispersal events  
9 have a major influence on the probability of plant colonization and persistence in habitat patches  
10 (Cain *et al.* 2000, Pearson and Dawson 2005, Kunstler *et al.* 2007). Therefore, plantations close  
11 to seed sources could be expected to have more active recruitment and successional dynamics  
12 than plantations far from seed sources (Hewitt and Kellman 2002, White *et al.* 2004). In  
13 summary, the ecological consequences of a forest plantation will be largely influenced by its  
14 position along abiotic, biotic, and dispersal distance gradients.

15         In this study, we conduct a large-scale assessment of the ecological impacts of forest  
16 plantations in mountain landscapes of southern Spain. For this, we analysed plant regeneration  
17 and diversity in 442 pine plantations plots covering a wide gradient of climatic conditions, stand  
18 density, and distance to natural forest fragments that act as seed sources. Plantations (mainly  
19 pines) cover millions of hectares in the Iberian Peninsula, as well as in most countries of the  
20 Mediterranean Basin, where they have been widely used to recover the forest surface area lost  
21 over thousands of years of human timber exploitation and conversion to agricultural lands  
22 (Pausas *et al.* 2004, FAO 2005). Fast-growing pines were considered an intermediate  
23 successional stage between the transitional shrubs and the mature tree community, and therefore

1 assumed to facilitate the introduction of late-successional hardwoods (Barbéro *et al.* 1998,  
2 Pausas *et al.* 2004, Barčić *et al.* 2006). However, since most reforestation initiatives were not  
3 followed up with subsequent management or monitoring, it is unknown to what extent  
4 plantations successfully promote the recovery of native vegetation. Specifically, we ask: 1) what  
5 is, on average, the abundance of tree regeneration and the plant diversity of pine plantations, in  
6 comparison to native broadleaf forests? and 2) how does regeneration and diversity in plantations  
7 vary along gradients of climatic conditions, stand density, and distance to seed sources? The  
8 answers to these questions represent critical information to develop efficient strategies of  
9 plantation management that integrate the environmental heterogeneity found in the extensive  
10 areas covered by this type of novel ecosystem.

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## MATERIAL AND METHODS

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### *Study site*

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The study was conducted at the Sierra Nevada National Park (Andalusia, SE Spain; Fig. 1). The climate is Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought (July-August). Precipitation is concentrated mainly in autumn and spring. Sierra Nevada includes an altitudinal gradient from around 300 m to 3482 m a.s.l. (the highest peak in the Iberian Peninsula). Precipitation increases and temperature drops with altitude (García-Canseco 2001). Annual precipitation ranges from less than 250 mm in the lowest parts of the mountain range to more than 700 mm in the highest peaks. Winter precipitation is mainly in the form of snow above 2000 m of altitude. Mean annual temperatures vary from 12-16°C in the low mountain to 8-12°C at 2000-2500 m, and to < 0°C above 3000 m a.s.l..

1 Additionally, the complex orography of the mountains causes strong climatic contrasts between  
2 the sunny and dry south-facing slopes and the shaded and wetter north-facing slopes.

3 The main native forests of Sierra Nevada are stands dominated by the evergreen oak  
4 *Quercus ilex* subsp. *ballota* (Desf.) Samp. (which represents about 13% of the forested cover of  
5 the national park), and stands dominated by the deciduous oak *Quercus pyrenaica* Willd. (5.5%  
6 of the forested cover of the park) accompanied by other deciduous tree species such as *Acer*  
7 *opalus* subsp. *granatense* (Boiss.) Font Quer & Rothm and *Sorbus aria* (Pérez-Raya *et al.* 2001).  
8 Plantations of four pine species (*Pinus halepensis* Mill., *Pinus pinaster* Ait., *Pinus nigra* Arnold.  
9 subsp. *salzmannii* (Dunal) Franco, and *Pinus sylvestris* L.) represent 79% of the forested cover of  
10 the national park. These plantations were established mainly during the period 1960-1980 on  
11 highly degraded, extensive agricultural landscapes abandoned after the Spanish Civil War (1936-  
12 1939). Soil preparation in most plantations consisted of terracing, and 1-2 year old pines were  
13 planted in 1 m<sup>2</sup> manually dug holes. *Pinus halepensis* was the pine species most commonly used  
14 in low-altitude plantations (<1300 m a.s.l.) due to its drought tolerance, whereas montane pines  
15 (*P. nigra* and *P. sylvestris*) were the most widely used species in high-altitude plantations (>1900  
16 m a.s.l.). The four pine species are found in plantations at intermediate altitudes (1300-1900 m  
17 a.s.l.), sometimes forming mixed stands. Planted pines can also appear intermingled with  
18 remnants of natural *Quercus* forests at low-mid altitudes, and autochthonous *P. sylvestris* var.  
19 *nevadensis* forests in the high mountain.

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#### *Data set*

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We analysed a large data set from a forest inventory conducted for the Sierra Nevada  
National Park during 2004-2005. The forest inventory included an extensive network of 600

1 long-term permanent plots (20 x 20 m) distributed within the main forest units of the park: pine  
2 plantations, evergreen *Q. ilex* forests, and deciduous broadleaf forests. The network of plots is a  
3 random sample stratified by land cover and altitude, covering a gradient of 974 to 2439 m a.s.l.  
4 Within the 20 x 20 m plots, each live tree with a diameter at breast height (DBH) > 7.5 cm was  
5 mapped, its species identity annotated and the DBH measured. Two additional circular subplots  
6 were established within each larger plot: a 5-m radius plot (78.5 m<sup>2</sup> in area) for the estimation of  
7 the number of seedlings (DBH < 2.5 cm and height < 1.3 m) and saplings (DBH = 2.5-7.5 cm) of  
8 tree species, and a 10-m radius plot (314 m<sup>2</sup> in area) for estimation of understory herbaceous  
9 and woody species composition and abundance. For resprouting species (i.e., *Quercus* sp.) our  
10 approach does not allow a clear distinction between ramets and genets. This difficulty  
11 nevertheless did not significantly affect the main conclusions of the paper on regeneration  
12 patterns, which were based more on relative differences between natural forests and plantations,  
13 and among plantation plots, than on absolute numbers of recruits.

14 Our analyses of natural regeneration and diversity along gradients focused on the 442  
15 plots of the network in which planted pines form part of the canopy (Fig. 1). About 85% of the  
16 442 plantation plots had a canopy composed exclusively by planted pines, whereas the remaining  
17 15% of the plots had some representation of natural pine and broadleaf tree species (mainly *P.*  
18 *sylvestris* var. *nevadensis*, *Q. ilex*, *Q. pyrenaica*, *A. opalus* subsp. *granatense*, and *S. aria*). Pine  
19 density ranged from 25 to 2800 pines/ha (basal area = 0.01-77.4 m<sup>2</sup>/ha). Natural broadleaf forest  
20 plots were used only as a reference to compare mean values of regeneration and diversity with  
21 plantation plots (n = 45 for *Q. ilex* forests, n = 26 for deciduous forests; Fig. 1). Tree density  
22 ranged between 26 and 721 trees/ha (basal area = 0.04-18.9 m<sup>2</sup>/ha) in *Q. ilex* forests, and  
23 between 26 and 1038 trees/ha (basal area = 0.01-23.1 m<sup>2</sup>/ha) in deciduous forests.



1 Each of the 442 plantation plots was characterized with 19 topographic and climatic  
2 variables. Raster maps and plot locations (UTM coordinates) were combined to determine the  
3 values of each abiotic variable in each plot using ArcView Gis 9.2 (ESRI Inc., Redlands, USA,  
4 2000). The 19 abiotic variables were: *altitude* (determined from a digital elevation model with a  
5 10-m resolution); *annual* and seasonal (i.e., *spring*, *summer*, *fall*, and *winter*) *precipitation* (from  
6 Sánchez et al. 1999); annual *mean*, *maximum*, and *minimum temperature* (from Sánchez et al.  
7 1999); *annual* and seasonal (i.e., *spring*, *summer*, *fall*, and *winter*) *radiation* (obtained from a  
8 digital elevation model with a 10-m resolution); *annual potential evapotranspiration*, measured  
9 as a function of mean temperature (Thornthwaite 1948); *annual water deficit*, calculated as the  
10 sum of negative differences between annual precipitation and potential evapotranspiration;  
11 *annual water surplus*, calculated as the sum of positive differences between annual precipitation  
12 and potential evapotranspiration; *drought length*, taken as the number of months in which  
13 potential evapotranspiration exceeded precipitation; and *weeks with snow*, calculated as the  
14 average number of weeks with snow per year (period 2001-2007) using the Normalized  
15 Difference Snow Index (NDSI) from MODIS images (Salomonson and Appel 2004). The  
16 relationship among the 19 abiotic variables were explored with Principal Component Analyses  
17 (PCA). The first axis of the PCA (explaining 67.7% of the variance) was strongly correlated with  
18 altitude, precipitation, temperature, and drought indices. The second axis (explaining 15.6% of  
19 the variance) was strongly correlated with radiation variables. Therefore, we chose for our  
20 modelling analyses two variables representative of each of the two axes: altitude and annual  
21 radiation. Altitude summarizes the simultaneous variation in precipitation and temperature  
22 associated with altitudinal gradients in mountain areas, whereas annual radiation summarizes the  
23 variation in solar irradiance that occurs due to variations in slope (higher radiation at low slopes),

1 aspect (higher radiation in southern orientations) and altitude (higher radiations at high altitudes).  
2 We considered these two variables to represent a synthesis of the complex climatic regimes of  
3 the Sierra Nevada mountains.

4 For each inventory plot, we also calculated the distance to the nearest natural *Q. ilex*  
5 forest using a GIS and a digital vegetation map (Pérez-Raya *et al.* 2001). In this way, we aimed  
6 to evaluate the importance of the distance to seed sources in the re-colonization of plantations by  
7 this species, the dominant broadleaf tree at the landscape scale in Sierra Nevada.

8

#### 9 *A maximum-likelihood analyses of regeneration and diversity*

10 We used likelihood methods and model selection as an alternative to traditional  
11 hypothesis testing (Johnson and Omland 2004, Canham and Uriarte 2006) for analysis of our  
12 data. Following the principles of likelihood estimation, we estimated model parameters that  
13 maximized the likelihood of observing the regeneration and diversity data measured in the field  
14 given a suite of alternate models.

15 *Regeneration models.*- We conducted separate analyses of seedling density (i.e., number  
16 of seedlings [DBH < 2.5 cm and height < 1.3 m] in the 5-m radius subplots) for the 5 most  
17 common tree species (*Q. ilex*, *P. halepensis*, *P. pinaster*, *P. nigra*, and *P. sylvestris*). These  
18 species comprised 94.3% of the total number of seedlings found in the 442 plantation plots (n =  
19 4215 seedlings). Seedlings of deciduous native tree species were not analysed due to insufficient  
20 number. We also conducted an additional analysis for the density of *Q. ilex* saplings (DBH = 2.5-  
21 7.5 cm). This analysis was not conducted for pine saplings because we could not distinguish  
22 which of these small pines were natural recruits and which were suppressed adult planted pines.

1 In fact, most pine saplings appeared in plantations with extremely high (> 2000 pines/ha) canopy  
2 densities.

3 Our analyses of tree seedling and sapling density in plantations estimated three terms: 1)  
4 average potential regeneration (PotReg, in number of individuals per 5-m radius plot), and three  
5 sets of scalar modifiers ranging from 0 to 1 that quantify the effects on average potential  
6 regeneration of 2) local climatic conditions (expressed in terms of altitude and annual radiation),  
7 3) stand density (number of pines per ha), and 4) distance (in m) to the nearest seed source. This  
8 last scalar was considered only for analyses of *Q. ilex* seedlings and saplings, since seedlings of  
9 pine species never appeared in plots without conspecifics in the canopy (i.e., distance to seed  
10 sources equalled zero in all cases). Our *full model* has the following form:

$$11 \text{ Regeneration} = \text{PotReg} \times \text{Climatic effect} \times \text{Density effect} \times \text{Distance effect} \quad (1)$$

12 *Potential regeneration* (PotReg) in this model represents the expected number of  
13 seedlings/saplings in a 5-m radius plot when the other factors are at optimal values. The *climatic*  
14 *effect* was modelled using a bivariate Gaussian function:

$$15 \text{ Climatic effect} = \exp \left[ -\frac{1}{2} \left( \frac{A - X1_0}{X1_b} \right)^2 \right] * \exp \left[ -\frac{1}{2} \left( \frac{R_{an} - X2_0}{X2_b} \right)^2 \right] \quad (2)$$

16 where  $X1_0$  and  $X2_0$  are the altitude (A) and annual radiation ( $R_{an}$ ) values, respectively, at which  
17 maximum potential seedling/sapling number occurs; and  $X1_b$  and  $X2_b$  are estimated parameters  
18 that control the breadth of the function (i.e., the variance of the normal distribution). Equation 2  
19 produces the classic Gaussian distribution of species performance along an environmental axis  
20 usually assumed to describe vegetation-environment relationships (e.g., Curtis 1959, Whittaker  
21 1975, Gauch 1982), but can also produce sigmoidal, monotonic curves within restricted ranges of

1 either axis. We also tested univariate functions in which terms for one of the two axes were  
2 dropped from the analysis.

3 The *density effect* was modelled using a univariate Gaussian function:

$$4 \text{ Density effect} = \exp \left[ -\frac{1}{2} \left( \frac{\text{Density} - X3_0}{X3_b} \right)^2 \right] \quad (3)$$

5 where  $X3_0$  represents the pine density (pines/ha) at which maximum seedling/sapling density  
6 occurs, and  $X3_b$  controls the breadth of the function. The *density effect* was also tested using pine  
7 basal area instead of density as predictor, but in no case were the models a better fit (data not  
8 shown).

9 We also tested a variant of the Eq. 3 in which the *density effect* was allowed to vary as a  
10 function of the climatic conditions of the plot. This effect is independent of the underlying direct  
11 effect of climate on potential regeneration (i.e., the *climatic effect*). For this, the mode term ( $X3_0$ )  
12 in Eq. 3 was allowed to vary as a function of climatic variables (either altitude or annual  
13 radiation):

$$14 X3_0 = X3_0 + \gamma * \text{Climatic variable} \quad (4)$$

15 If  $\gamma > 0$ , then maximum seedling/sapling density (i.e., the mode of the function) is reached at  
16 higher pine densities with increasing altitude or radiation. If  $\gamma < 0$ , then maximum  
17 seedling/sapling density is reached at lower pine densities with increasing altitude or radiation.

18 We tested two alternative forms to model the *distance effect*: a Weibull dispersal function  
19 (the most used in previous studies; see Ribbens *et al.* 1994, Clark *et al.* 1998, LePage *et al.* 2000)  
20 and a lognormal dispersal function (suggested by Greene *et al.* 2004 to fit empirical data as well  
21 as or better than Weibull functions). However, because the lognormal function was in no case a

1 better fit to the data than the Weibull function (results not shown for simplicity), we selected the  
2 Weibull dispersal kernel to model the *distance effect*. The Weibull function has the form:

$$3 \text{ Distance effect} = \exp(-\alpha * \text{Distance}^\beta) \quad (5)$$

4 where  $\alpha$  controls the rate of decrease of seedling/sapling density with distance, and  $\beta$  controls the  
5 shape of the function.

6 *Diversity models.* - We conducted separate analyses for two different diversity indexes:  
7 species richness (or species number) and the Shannon's (H') diversity index (a more complex  
8 index that combines species richness and relative abundance), both calculated at the 10-m radius  
9 plot scale. Models were run for the two indexes because some authors have argued that species  
10 richness and evenness may be independent, and thus should be treated separately (Weiher and  
11 Keddy 1999, Bell 2000, Ma 2005, González-Megías 2007). Models were run for all species  
12 together and for species sub-groups, in order to explore differences among life-forms and  
13 dispersal syndromes. Plant species were classified into three different functional groups: fleshy-  
14 fruited woody species (with endozoochorous dispersal), dry-fruited woody species (with  
15 dispersal syndromes other than endozoochory, mainly abiotic dispersal), and herbaceous species  
16 (Appendix A). Herbaceous species were not divided into subgroups according to dispersal  
17 syndrome because most of them (>95%) were dry-fruited and abiotically dispersed. Following  
18 the same reasoning as for regeneration, our analyses of richness and H' index estimated three  
19 terms: 1) average potential richness (PotRich) or H' index (PotH'), and two sets of scalar  
20 modifiers ranging from 0 to 1 that quantify the effects on PotRich/PotH' of 2) local climatic  
21 conditions (altitude and annual radiation), and 2) plantation density (pines/ha). The *climatic* and  
22 *density effects* on diversity were modelled using the same forms as in Eqs. 2, 3 and 4.

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1 *Parameter estimation, model comparison, and model evaluation*

2 We first compared evidence for each of the three independent factors (climate, stand  
3 density, distance to seed sources) separately by comparing the Akaike Information Criterion  
4 (AIC) of their regression models to the AIC of the value of a null model (i.e., mean or intercept-  
5 only model). Null models were also run for total regeneration (i.e., number of seedlings/saplings  
6 of all tree species together) in both plantation and natural forest plots, as well as for richness and  
7 H' index in natural forest plots, in order to compare mean values of natural regeneration and  
8 diversity in pine plantations vs. natural broadleaf forests. We then tested increasingly complex  
9 models by combining sets of independent factors for which there was evidence (as measured by  
10 AIC) of univariate effects. The absolute magnitude of the differences in AIC between alternate  
11 models ( $\Delta AIC$ ) provides an objective measure of the strength of empirical support for the  
12 competing models.  $\Delta AIC$  values were also used to derive the Akaike weights ( $w_i$ ) for the set of  
13 candidate models (Burnham and Anderson 2002). The Akaike weight of model  $i$  can be  
14 interpreted as the expected probability of that model being selected as best when repeated  
15 independent samples are taken from the same population. The best model is considered to be  
16 clearly superior to the other candidate models when its  $w_i \geq 0.9$ .

17 The number of recruits (i.e., seedlings or saplings) in a 5-m radius plot was assumed to  
18 follow a zero-inflated Poisson (ZIP) distribution. By using this distribution, we modelled  
19 regeneration as the result of two distinct processes: first, the occurrence of recruitment, and  
20 second, the number of recruits conditional on the occurrence of recruitment. The ZIP function  
21 has the form:

$$22 \quad p(Y = y_i) = \begin{cases} pz + (1-pz)\exp^{-\lambda}, & y_i = 0 \\ (1-pz)\frac{\lambda_i^{y_i}}{y_i!}\exp^{-\lambda}, & y_i > 0 \end{cases} \quad (6)$$

1 where  $y_i$  represents the number of recruits in plot  $i$ ,  $p_z$  represents a constant probability across the  
2 dataset of getting zero recruits (structural or supplementary zeros), and  $\lambda$  is the mean of the  
3 Poisson distribution (modelled here as a function of climatic, density, and distance effects). Zero-  
4 inflated distributions have been recommended for the modelling of processes that, like tree  
5 recruitment, are often characterized by an excess number of zero counts that cannot be  
6 accommodated by traditional discrete probability distributions (i.e., Poisson distribution;  
7 Lambert 1992, Rathbun and Fei 2006, Fortin and DeBlois 2007). For species richness, we  
8 assumed a Poisson error structure (since the low number of zeros did not require the use of zero-  
9 inflated models). H' index values were modelled using a normal error distribution.

10 We used simulated annealing, a global optimisation procedure, to determine the most  
11 likely parameters (i.e., the parameters that maximize the log-likelihood) given our observed data  
12 (Goffe et al. 1994). The  $R^2$  of the regression ( $1 - \text{SSE}/\text{SST}$ ) of observed vs. predicted values was  
13 used as a measure of goodness of fit (SSE, sum of squares error; SST, sum of squares total). We  
14 used asymptotic two-unit support intervals to assess the strength of evidence for individual  
15 maximum likelihood parameter estimates (Edwards 1992). A support interval is defined as the  
16 range of the parameter value that results in less than a two-unit difference in AIC. It is roughly  
17 equivalent to a 95% support limit defined using a likelihood ratio test (Hilborn and Mangel  
18 1997). All analyses were performed using R v 2.5.0 (R Development Core Team 2006) and the  
19 *likelihood* package v 1.1 (available at [http://www.ecostudies.org/lme\\_R\\_code\\_tutorials.html](http://www.ecostudies.org/lme_R_code_tutorials.html)).

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## RESULTS

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### *Regeneration*

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The comparison of the mean models (i.e., null models) for pine plantations and natural

1 stands indicates that the probability of finding no regeneration was higher in plantation plots ( $p_z$   
 2 = 0.54 for seedlings,  $p_z = 0.89$  for saplings) than in *Q. ilex* and deciduous plots ( $p_z \sim 0.2$  for  
 3 seedlings,  $p_z \sim 0.5$ - $0.6$  for saplings; Appendix B). Seedling density in plantations was on average  
 4 four times lower (PotReg = 20.96 seedlings per 5-m radius plot [i.e., 0.27 seedlings/m<sup>2</sup>];  
 5 Appendix A) than in natural *Q. ilex* (PotReg = 81.34, 1.03 seedlings/m<sup>2</sup>) and deciduous forests  
 6 (PotReg = 77.92, 1.01 seedlings/m<sup>2</sup>), whereas sapling density was half (PotReg = 6.13 saplings  
 7 per 5-m radius plot [i.e., 0.08 saplings/m<sup>2</sup>]; Appendix B) that of native *Q. ilex* forests (PotReg =  
 8 12.97, 0.16 saplings/m<sup>2</sup>) but similar to deciduous forests (PotReg = 4.83, 0.06 saplings/m<sup>2</sup>).  
 9 However, seedling density values varied strongly among plantation plots along axes of altitude,  
 10 radiation, stand density and, in the case of *Q. ilex*, also distance to seed sources, as indicated by  
 11 the best models of each of the 5 species tested ( $w_i > 0.9$  for the *full models*; Table 1).

12 All species showed the expected Gaussian curve in response to altitude (Fig. 2a). The  
 13 lack of overlap among species in the value of the mode of the curve (parameter  $XA_0$  in Appendix  
 14 C) indicates a clear segregation along this gradient (from lower to higher altitude): *P. halepensis*  
 15 < *P. pinaster* < *Q. ilex* seedlings < *Q. ilex* saplings < *P. nigra* < *P. sylvestris*. Most species also  
 16 showed a Gaussian response along the radiation gradient (Fig. 2b). Only for *Q. ilex* did our data  
 17 fail to support a radiation effect on seedling abundance. Along this abiotic gradient, however, the  
 18 mode of the curve often overlapped among species, maximum densities occurring in most cases  
 19 at intermediate radiation levels ( $XR_0 \sim 4.5$ - $5.5$  GJ/m<sup>2</sup>; Appendix C).

20 Seedling species also segregated along a gradient of stand density: *P. halepensis* reached  
 21 maximum seedling densities at low values of pine density (0-100 pines/ha), tending to null  
 22 regeneration within 1000-1500 pines/ha (Fig. 2c; Appendix C). The three remaining pine species  
 23 and *Q. ilex* saplings had recruitment peaks ( $XD_0$  parameter) at densities between 400-900



1 pines/ha, tending to null regeneration within 1500-2000 pines/ha. Finally, *Q. ilex* seedling  
2 abundance peaked at 1100-1300 pines/ha, some seedlings recruiting at even 3000 pines/ha.  
3 Moreover, for three of the five tree species, our data supported a model in which the mode of the  
4 density effect was allowed to vary as a function of the climatic conditions of the plot (Table 1).  
5 Thus, for *Q. ilex* seedlings and saplings, the maximum seedling abundance occurred at lower  
6 pine densities with decreasing altitude (i.e., decreasing precipitation and increasing temperature,  
7 positive values of the  $\gamma$  parameter; Fig. 3a,b and Appendix C). For *P. nigra* and *P. sylvestris*, the  
8 maximum seedling abundance occurred at lower pine densities with increasing annual radiation  
9 (negative values of the  $\gamma$  parameter; Fig. 3c,d).

10 In the case of *Q. ilex*, seedling and sapling abundance also depended heavily on the  
11 distance to the nearest seed source (i.e., natural *Q. ilex* forest), as indicated by the large decrease  
12 in AIC when distance effects were added to a model of climatic and density effects (Table 1).  
13 *Quercus ilex* recruitment in plantation plots decreased exponentially with distance to the nearest  
14 *Q. ilex* forest (Fig. 2d). The rate of decrease was much slower for *Q. ilex* seedlings than for *Q.*  
15 *ilex* saplings. Thus, whereas the predicted probability of finding a *Q. ilex* seedlings tended to  
16 zero within 4 km from the nearest seed source, for *Q. ilex* saplings it tended to zero within half  
17 the distance (2 km).

18 Altogether, the effects of climate, stand density, and dispersal distance determined that  
19 plantations at low (~ 1300 m a.s.l.) and middle altitudes (~ 1700 m a.s.l.) and with moderate  
20 stand densities (500-1000 pines/ha) had the highest seedling and sapling abundance, mainly of *Q.*  
21 *ilex*, but also of the four pine species (Fig. 4a,b). At these altitudinal levels, even the densest  
22 plantations had some regeneration thanks to the capacity of *Q. ilex* to recruit at even 3000  
23 pines/ha. On the contrary, high-altitude plantations (~ 2100 m a.s.l.) had much lower recruitment,

1 the seedling bank being largely dominated by *P. sylvestris* (Fig. 4c). At this altitude, plantations  
 2 with > 2000 pines/ha were totally devoid of regeneration.

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4

#### *Diversity*

5 The comparison of the mean models (i.e., null models) for plantations and natural stands  
 6 indicated that plantations had on average lower species richness (PotRich = 13.09 in the mean  
 7 model; Appendix B) than native *Q. ilex* (PotRich = 14.92) and deciduous forests (PotRich =  
 8 17.55). However, this lower richness was due mainly to a lower number of herbaceous species,  
 9 whereas the number of woody species (both fleshy-fruited and dry-fruited) was sometimes even  
 10 higher in plantations than in natural forests (Appendix B). Plantations had also a lower H' index  
 11 (PotH' = 1.47) than *Q. ilex* (PotH' = 1.77) and deciduous forests (PotH' = 1.81). However, this  
 12 lower value was again due primarily to a lower H' index of herbaceous species, whereas the H'  
 13 index for woody species (both fleshy-fruited and dry-fruited) was similar in the three forest  
 14 formations (support intervals overlapped among forest formations for PotH'<sub>WFleshy</sub> and PotH'<sub>WDry</sub>;  
 15 Appendix B).

16 Our data clearly supported a strong climatic and stand density effect on species richness  
 17 ( $w_i > 0.9$  for the *full models*; Table 2). Total species richness peaked at middle altitudes (Fig. 5a).  
 18 The altitudinal effect was stronger for the subgroup of fleshy-fruited woody species, as indicated  
 19 by a smaller breadth ( $XA_b$  parameter) of the Gaussian curve (Appendix D). Fleshy-fruited woody  
 20 species was also the only subgroup that responded to radiation, their richness decreasing roughly  
 21 linearly with increasing radiation (Fig. 5b). Stand density had a strong negative effect on species  
 22 richness of all groups. However, whereas the response curves of dry-fruited woody and  
 23 herbaceous species peaked at zero density values, maximum richness of fleshy-fruited woody

1 species occurred at a greater density ( $XD_0=455.78$  pines/ha; Appendix D) and decreased at a  
2 slower rate (larger  $XD_b$  parameter) with increasing density (Fig. 5c).

3 We found strong empirical support for an effect of both climate (only altitude) and stand  
4 density on the  $H'$  index of all species together and of dry-fruited woody species (Table 2). On the  
5 contrary, the most parsimonious models for fleshy-fruited woody and herbaceous species  
6 included only a climatic effect of both altitude and annual radiation (Table 2). The response of  
7 the  $H'$  indices to altitude was similar to that of richness estimators, with a peak at intermediate  
8 altitude and a stronger effect on the fleshy-fruited woody species subgroup (Fig. 5d). The effect  
9 of radiation on the  $H'$  index differed for fleshy-fruited and herbaceous species: whereas fleshy-  
10 fruited woody species decreased monotonically with increasing radiation (as occurred for  
11 richness), the  $H'$  index of herbaceous species peaked at intermediate radiation (Fig. 5e). Stand  
12 density had, as for richness, a strong negative effect on the  $H'$  index for all species grouped (Fig.  
13 5f). However, this effect was owed mainly to the effect on dry-fruited woody species, the only  
14 subgroup for which data supported a stand density effect. Our data did not support models in  
15 which the peak of maximum richness or  $H'$  index varied depending on the climatic conditions of  
16 the site (i.e., AIC did not improve with the addition of the  $\gamma$  term to the model; Table 2).

17 Altogether, the effects of climate and stand density determined that plantations at middle  
18 altitudinal levels and low tree densities (<500 pines/ha) had the highest values of richness and  $H'$   
19 index (Fig. 6).

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## DISCUSSION

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Our results indicate that pine plantations in Mediterranean mountain landscapes had, on average, less active regeneration and lower plant species diversity than natural broadleaf forests.

1 However, this general negative effect of plantations needs to be qualified, since it varied strongly  
2 depending on local climatic conditions, stand density, and distance to seed sources, as well as  
3 among plant species with different life-history traits.

4

#### 5 *Effects of pine plantations on tree regeneration*

6 We developed models that relate the seedling and sapling density of the most common  
7 tree species in plantation understoreys with the abiotic (climate, distance to seed sources) and  
8 biotic (stand density) characteristics of the plantation plots. For the five species tested, we found  
9 strong empirical support ( $w_i > 0.9$ ) for the *full model* that included all these factors as predictors  
10 of regeneration. Tree seedling density varied along the 3 gradients from virtually zero to values  
11 close to those found in natural forests of Sierra Nevada ( $\sim 1$  seedling/m<sup>2</sup>; Fig. 3). Therefore,  
12 regeneration dynamics in a particular plantation were highly dependent on the specific  
13 characteristics of the plot.

14 Plantations at low-mid altitudes had a more diverse and abundant seedling and sapling  
15 bank than high-altitude plantations (Fig. 4). The former showed a seedling bank dominated by *Q.*  
16 *ilex* and accompanied by several pine species (*P. halapensis*, *P. pinaster*, *P. nigra*), whereas the  
17 latter showed a virtually monospecific seedling bank of *P. sylvestris*. The fact that *P. sylvestris*  
18 had maximum seedling density at higher altitude than the other tree species is consistent with its  
19 domination of the treeline in Sierra Nevada, where extremely low temperatures and high  
20 radiation can limit the establishment of other pine and *Quercus* species. Based on the species  
21 composition of the seedling bank, high-mountain plantations could be expected to exhibit  
22 autosuccessional dynamics and perpetuate as monospecific *P. sylvestris* plantations. On the  
23 contrary, low-medium altitude plantations could be expected to follow a successional trajectory

1 towards the replacement of pine forests by oak or mixed pine-oak forests, as suggested by the  
2 much larger seedling numbers of *Q. ilex* than of any pine species. This pine-oak replacement is  
3 in agreement with previous studies conducted in Mediterranean areas (Retana *et al.* 1999,  
4 Lookingbill and Zavala 2000) and other parts of the world where pines and oaks are also major  
5 structural components of forest ecosystems (Zavala *et al.* 2007).

6 Stand density had a striking effect on regeneration throughout the whole altitudinal  
7 gradient. Seedling and sapling density of all 5 species peaked in the first half of the density  
8 gradient (<1500 pines/ha), tending quickly to zero above this level (Fig. 2c and 4). Only *Q. ilex*  
9 was able to recruit some seedlings in high-density plantations, probably as a result of its much  
10 higher shade-tolerance than pine species (Retana *et al.* 1999, Gómez-Aparicio *et al.* 2006,  
11 Niinemets and Valladares 2006). However, the transition of these seedlings to the sapling stage  
12 seems inhibited at such high densities, probably as a result of increasing light requirements with  
13 ontogeny not met in dense stands (Espelta *et al.* 1995). Densities over 1500 pines/ha clearly  
14 represented a biotic constraint to the recruitment process in the understorey of pine plantations.  
15 On the other extreme of the density gradient, we found that moderate plantation densities (500-  
16 1000 pines/ha) promoted recruitment of most species in comparison to low or null canopy cover.  
17 This finding suggests the existence of facilitative interactions in which tree seedlings benefit  
18 from the special abiotic conditions inside the forest stand (e.g., protection from excessive  
19 evapotranspiration, extreme temperatures, high radiation or strong winds, improved soil  
20 conditions). In fact, facilitation of plant establishment by a moderate canopy cover seems to be a  
21 common process in Mediterranean forests and shrublands (Gómez-Aparicio *et al.* 2004, Padilla  
22 and Pugnaire 2006, Gómez-Aparicio 2008). *Pinus halepensis* was the only tree species that did  
23 not benefit from a moderate pine density. This result agrees with the fact that this species is

1 considered the most drought-tolerant pine in the Mediterranean basin (Barberó *et al.* 1998), and  
2 that facilitation by neighbors is usually more common in stress-intolerant than in stress-tolerant  
3 species (Liancourt *et al.* 2005, Michalet *et al.* 2006, Gómez-Aparicio *et al.* 2008). Overall, our  
4 analyses reveal regeneration patterns that are consistent with a shift from facilitation to  
5 competition in the overstorey-understorey interaction along the stand density gradient. Therefore,  
6 the rationale behind the establishment of pine plantations in degraded Mediterranean systems -its  
7 nurse role of native vegetation- applies only over a relatively small fraction (<1000 pines/ha) of  
8 the entire density gradient found at the landscape scale.

9         It bears noting that we found support for the shift between facilitation and competition  
10 occurring at different stand density thresholds depending on local climate (Fig. 3). Thus,  
11 maximum recruitment of *Q. ilex* and mountain pines (*P. nigra* and *P. sylvestris*) occurred at  
12 lower stand densities with decreasing altitude (i.e., decreasing precipitation and increasing  
13 temperature) or increasing radiation. This result suggests that, under stressful conditions of low  
14 water availability (i.e., low altitude and high radiation) the potential benefits of the pine  
15 overstorey (e.g., amelioration of extreme climatic conditions) are quickly outweighed by the  
16 negative effects of competition for water. In fact, pine plantations have been shown to have a  
17 strong desiccating effect on soils due to high rainfall interception and water uptake (Maestre *et al.*  
18 2003, Bellot *et al.* 2004, Farley *et al.* 2005). However, when water availability increases (i.e.,  
19 high altitude and low radiation) competition for water relaxes, the shift from facilitation to  
20 competition occurs at higher stand densities, and net facilitation is found over a larger fraction of  
21 the density gradient. This line of reasoning is also supported by the fact that *P. halepensis* and *P.*  
22 *pinaster* (the two most drought-tolerant pines) were the only seedling species for which optimal  
23 stand density did not vary with climate, probably due to their higher ability to tolerate the

1 negative effects of competition for water with canopy trees. The verification of this mechanistic  
2 explanation requires, however, an experimental study that analyse how soil characteristics,  
3 microclimate, and seedling performance vary along gradients of pine densities.

4 Our study clearly indicates a prominent importance of distance to seed sources for the  
5 colonization of plantations by *Q. ilex*. Thus, seedling abundance diminished in 50% within the  
6 first 250 m from the nearest *Q. ilex* forest, and by 80% within 1 km (Fig. 2d). However, some  
7 seedlings were found at distances as far as 4 km from the nearest seed source, likely as a result of  
8 long-distance dispersal events. In fact, 4 km coincides with the maximum flight distance reported  
9 for jays, one of the main dispersers of *Quercus* sp. in Europe (European jay, *Garrulus glandarius*)  
10 and North America (blue jay, *Cyanocitta cristata* L.) (Bossema 1979, Johnson and Adkisson  
11 1985). Yet, the rate of long-distance dispersal events does not seem to be sufficient to maintain a  
12 sapling bank of *Q. ilex* in such remote patches, since the probability of sapling recruitment  
13 tended to zero within shorter distance (2 km). In heterogeneous Mediterranean landscapes, jays  
14 move acorns nonrandomly, avoiding some patches (e.g., shrublands and grasslands) and moving  
15 most acorns to pine stands, which in turn are high-quality habitats for emergence and survival of  
16 *Q. ilex* seedlings (Gómez 2003, 2004). This effective directed dispersal, together with the  
17 abundance of *Q. ilex* forests at the landscape scale (>70% of the 442 plantation plots were at  $\leq 2$   
18 km from the nearest *Q. ilex* fragment), may be crucial for the successional dynamics towards oak  
19 forests that many pine plantations appear to undergo in Sierra Nevada.

#### 21 *Effects of plantations on the diversity of vascular plants*

22 Pine plantations had on average lower total plant richness and H' index values than native  
23 stands, especially when compared with deciduous broadleaf forests. However, in a detailed

1 analysis, this negative effect appeared only for herbaceous species, and not for woody species.  
2 The negative effect on herbaceous species is probably a result of the much higher tree density of  
3 plantations in comparison to native fragments, which in turn implies lower understorey light  
4 levels usually responsible of low herbaceous richness and cover (Harrington and Edwards 1999,  
5 Thomas *et al.* 1999). In any case, pine plantations were not “biological deserts”, and several  
6 woody and herbaceous species were able to survive within these forest stands. However, plant  
7 diversity was very heterogeneous among plantation plots, depending on their local climatic and  
8 density characteristics.

9 Both species richness and  $H'$  index values showed a hump-shaped pattern distribution  
10 along the altitudinal gradient (Fig. 5a,d). This pattern seems to be the most common when entire  
11 altitudinal gradients are sampled (as in this study) due to both higher productivity and lower  
12 human impact at mid-altitudinal habitats (Rahbek 2005, Nogués-Bravo *et al.* 2008). Radiation  
13 had a more modest effect than altitude on both richness and  $H'$  index values, its effect being  
14 restricted primarily to fleshy-fruited woody species. In fact, this group, much less abundant than  
15 dry-fruited and herbaceous species in all cases, was also the most affected by climatic gradients,  
16 being restricted largely to areas at intermediate altitudes and with low radiation (*i.e.*, north-facing  
17 slopes, valley floors). Therefore, mid-altitude plantations had not only higher species richness  
18 and evenness, but also higher relative abundance of fleshy-fruited woody species, than did  
19 plantations at the two extremes of the altitude gradient.

20 Stand density had a strong effect on total species richness and evenness, which decreased  
21 monotonically along the density gradient (Fig. 6). The impoverished plant diversity of high-  
22 density plantations was presumably due to higher seed and establishment limitation than in low-  
23 density plantations. On the one hand, bird abundance and richness is in general negatively



1 affected by high canopy densities (especially for jays), thereby reducing the seed flow entering  
2 plantations (Vallauri *et al.* 2002, De la Montaña *et al.* 2006). A very dense stand structure is also  
3 probably a direct obstacle to seed dispersal by wind. On the other hand, thinning experiments  
4 have shown species richness to respond positively to tree removal due to competition release  
5 and an increased availability of resources (light, water, and nutrients), allowing a greater number  
6 of understorey species to persist (Thomas *et al.* 1999, Cummings *et al.* 2007). It is likely that  
7 native species are not adapted to establish in such competitive environments, since natural forests  
8 of the area rarely exceed 1000 trees/ha.

9         When species subgroups were considered, richness of dry-fruited and herbaceous species  
10 followed a variation pattern along the density gradient similar to that of total species richness -  
11 that is, a monotonically decrease with increasing stand density. On the contrary, richness of  
12 fleshy-fruited bird-dispersed species peaked at a moderate tree density (about 500 pines/ha) and  
13 was less negatively affected by stand density than in the other subgroups (i.e., richness at  
14 maximum stand density reduced only to about 40% of potential, instead of to 20% as in the other  
15 subgroups; Fig. 5b). These among-group differences might be influenced by the relationship  
16 between dispersal mode and successional status (Huston and Smith 1987). A large number of  
17 Mediterranean fleshy-fruited woody species are late-successional shade-tolerant species, whereas  
18 pioneer woody species (e.g., *Cistaceae*, *Labiatae*, *Leguminosae*) usually have dry fruits (Herrera  
19 1995). Therefore, fleshy-fruited species will have a comparatively higher probability of  
20 persisting in the dark understorey of dense plantations than light-demanding dry-fruited woody  
21 and herbaceous species. Because shade-tolerance is negatively correlated with drought-tolerance  
22 (Niinemets and Valladares 2007), fleshy-fruited species will also benefit more than any other  
23 group from the mild microclimate generated by a moderate canopy density.

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*Implications for management of pine plantations in Mediterranean landscapes*

In areas such as the Mediterranean Basin, where millions of hectares are covered with plantations, there is an increasing concern to reconvert them into more natural forests with active regeneration, high biodiversity levels, and high resilience to disturbances such as pests and fires (Maestre and Cortina 2004, Lamb et al. 2005, Vallejo et al. 2006). Our study indicates that, because regeneration dynamics and plant diversity of pine plantations in heterogeneous Mediterranean mountains varies broadly along abiotic and biotic gradients, plantations at different points along these gradients will require different management strategies.

Active management will be urgently required in high-density plantations (>1500 pines/ha) with arrested succession, where excessive pine density causes a net overstorey-understorey competitive interaction and limits seed inputs from both local (due to a poor understorey) and external sources. Thinning should be prescribed to allow the entrance of light, seeds, and dispersers, redirecting plantations towards more natural densities where facilitative interactions predominate. Densities of 500-1000 pines/ha seem to offer the best compromise between high seedling and sapling densities of most tree species, and high diversity levels of both woody and herbaceous species. However, thinning levels should be adjusted to the climatic conditions of the site. More intense thinning will be necessary under more stressful climatic conditions, but consistently leaving a residual density (at least 500 pines/ha) that minimizes the costs of negative interactions while maximizing the benefits of habitat amelioration by canopy trees.

On the other hand, passive management might be recommended for plantations with low and moderate stand density, since they can be considered transient systems with active successional dynamics. When at low and mid altitudes, these plantations would be expected to

1 change towards oak or pine-oak forests, with the coexistence of these two genera being  
2 determined by the stress level (oak dominance being promoted at mesic sites due to greater  
3 shade-tolerance) and the frequency of disturbance (disturbance promoting pine persistence;  
4 Zavala *et al.* 2000, Zavala and Zea 2004). When at high altitudes, these plantations would be  
5 expected to persist as pine forests dominated by *P. sylvestris*, the natural forest formations in the  
6 Sierra Nevada treeline.

7 Management strategies should also take into account that spontaneous colonization of a  
8 plantation depends heavily on its distance to natural forest fragments that act as seed sources, as  
9 well as on the dispersal ability of the species inhabiting such forests. Thus, among the pool of  
10 native tree species available at the landscape scale in Sierra Nevada, *Q. ilex* was the only  
11 broadleaf species abundantly found in plantation understoreys. Other species such as *Q.*  
12 *pyrenaica*, *A. opalus* subsp. *granatense*, or *S. aria* were basically absent, probably due to seed  
13 limitation derived from their low regional abundance (most plantations being too far from seed  
14 sources of these species) and/or less effective dispersal systems (i.e., wind dispersal in *Acer*). In  
15 fact, previous studies indicate that, when seeds are available, all these tree species have high  
16 probability of seedling and sapling establishment under moderate shade (as that found in many  
17 pine plantations; Gómez-Aparicio *et al.* 2005, Puerta-Piñero *et al.* 2007, Mendoza 2008).  
18 Enrichment planting will therefore be necessary to increase the diversity and abundance of the  
19 seedling bank of pine plantations and recover the mixed natural forests of Sierra Nevada, where  
20 *Pinus*, *Quercus*, *Acer* and *Sorbus* species coexist. Planting will be especially needed in  
21 plantations farther than 2 km from the nearest *Q. ilex* forest, where even successful colonization  
22 of *Q. ilex* is unlikely. Clearly, seed availability is a major limiting factor in most restoration  
23 activities (Young *et al.* 2001), making seed dispersal a key topic in the theoretical grounds of

1 restoration ecology (Howe and Miriti 2004) and enrichment planting a key activity in restoration  
2 practice (e.g., Gardiner et al. 2004, McCament and McCarthy 2005).

3       Because the ecological characteristics of plantations are strongly heterogeneous at the  
4 landscape scale, their use as restoration tools could fail if we do not incorporate the sources of  
5 such variability into management planning. We are confident that the results presented in this  
6 study will contribute to avoid oversimplification and promote the perception of plantations as  
7 dynamic systems where successional trajectories and diversity levels are determined by abiotic  
8 constraints, complex balances of competitive and facilitative interactions, the spatial  
9 configuration of native seed sources, and species life-history traits (dispersal system, shade and  
10 drought tolerance).

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TABLE 1. Comparison of the alternate models of regeneration (i.e., seedling and sapling density) for the 5 most common tree species in plantation understoreys (n = 442 plots).  $QUIL_{SDL}$ , *Q. ilex* seedlings;  $QUIL_{SAP}$ , saplings;  $PIHA_{SDL}$ , *P. halepensis* seedlings;  $PIPI_{SDL}$ , *P. pinaster* seedlings,  $PINI_{SDL}$ , *P. nigra* seedlings;  $PISI_{SDL}$ , *P. sylvestris* seedlings). The best model (lowest AIC,  $\Delta AIC=0$ ) is indicated in boldface type.

Species	Model	AIC <sub>c</sub>	$\Delta AIC_c$	$\omega_i$	Climatic axes	$\gamma$	NP	R <sup>2</sup>
$QUIL_{SDL}$	<b>Full</b>	<b>3841.05</b>	<b>0.00</b>	<b>1.00E+00</b>	A	Y [A]	11	0.25
	Density + Climatic	4151.06	310.01	4.81E-68			9	
	Dispersal + Climatic	4074.43	233.38	2.10E-51			8	
	Dispersal + Density	4246.81	405.76	7.77E-89			7	
	Climatic	4257.60	416.55	3.53E-91			6	
	Density	4860.90	1019.85	3.49E-222			4	
	Dispersal	4419.10	578.05	3.01E-126			4	
	Null	5020.09	1179.04	9.43E-257			2	
$QUIL_{SAP}$	<b>Full</b>	<b>437.14</b>	<b>0.00</b>	<b>9.04E-01</b>	A, R	Y [A]	11	0.20
	Density + Climatic	444.19	7.05	2.66E-02			9	
	Dispersal + Climatic	442.32	5.18	6.78E-02			8	
	Dispersal + Density	451.02	13.88	8.75E-04			7	
	Climatic	452.16	15.02	4.95E-04			6	
	Density	475.06	37.92	5.27E-09			4	
	Dispersal	454.70	17.56	1.39E-04			4	
	Null	486.74	49.60	1.53E-11			2	
$PIHA_{SDL}$	<b>Full</b>	<b>301.54</b>	<b>0.00</b>	<b>1.00E+00</b>	A, R	N	8	0.30
	Climatic	358.68	57.14	3.91E-13			6	
	Density	362.98	61.44	4.55E-14			4	
	Null	394.51	92.97	6.48E-21			2	
$PIPI_{SDL}$	<b>Full</b>	<b>963.20</b>	<b>0.00</b>	<b>1.00E+00</b>	A, R	N	8	0.37
	Climatic	1074.45	111.3	6.96E-25			6	
	Density	1136.32	173.1	2.56E-38			4	
	Null	1408.12	444.9	2.44E-97			2	
$PINI_{SDL}$	<b>Full</b>	<b>238.45</b>	<b>0.00</b>	<b>1.00E+00</b>	A, R	Y [R]	9	0.79
	Climatic	271.34	32.89	7.21E-08			6	
	Density	343.91	105.46	1.26E-23			4	
	Null	376.41	137.96	1.10E-30			2	
$PISI_{SDL}$	<b>Full</b>	<b>808.86</b>	<b>0.00</b>	<b>1.00E+00</b>	A, R	Y [R]	9	0.48
	Climatic	952.97	144.11	5.09E-32			6	
	Density	1068.00	259.14	5.35E-57			4	
	Null	1169.99	361.13	3.82E-79			2	

Notes: NP is the total number of parameters in the best model;  $\omega_i$  is the Akaike weight for each competing model; and  $R^2 = 1 - SSE/SST$  for the relationship between predicted and observed growth. The *Climatic axes* column indicates whether the best model incorporates terms for effects of altitude (A), annual radiation (R), or both. The  $\gamma$  column indicates whether (Y, yes; N, no) the best model also included a term that allows sensitivity to pine density to vary with climatic conditions (either altitude [A] or annual radiation [R]).

TABLE 2. Comparison of the alternate models of species richness and biodiversity (Shannon's index,  $H'$ ) in plantation understoreys ( $n = 442$  plots). Models were run for all species together and separated into three subgroups (fleshy-fruited woody species, dry-fruited woody species, and herbaceous species). The best model (lowest AIC,  $\Delta AIC=0$ ) is indicated in boldface type.

Variable	Model	AIC <sub>c</sub>	$\Delta AIC_c$	$\omega_i$	Climatic axes	$\gamma$	NP	R <sup>2</sup>
Richness <sub>All</sub>	<b>Full</b>	<b>2675.23</b>	<b>0.00</b>	<b>1.00E+00</b>	A, R	N	7	0.36
	Climatic	2869.33	194.10	7.11E-43			5	
	Density	2848.58	173.35	2.28E-38			3	
	Null	3091.04	415.81	5.11E-91			1	
Richness <sub>SWFleshy</sub>	<b>Full</b>	<b>1489.24</b>	<b>0.00</b>	<b>9.84E-01</b>	A, R	N	7	0.31
	Climatic	1497.44	8.21	1.63E-02			5	
	Density	1774.51	285.27	1.11E-62			3	
	Null	1810.92	321.68	1.38E-70			1	
Richness <sub>SWDry</sub>	<b>Full</b>	<b>2106.08</b>	<b>0.00</b>	<b>1.00E+00</b>	A	N	6	0.31
	Climatic	2216.58	110.51	1.01E-24			3	
	Density	2178.37	72.29	2.01E-16			3	
	Null	2582.01	475.93	4.50E-104			1	
Richness <sub>Herbaceous</sub>	<b>Full</b>	<b>2071.28</b>	<b>0.00</b>	<b>1.00E+00</b>	A	N	6	0.14
	Climatic	2147.83	76.55	2.38E-17			3	
	Density	2105.16	33.88	4.40E-08			3	
	Null	2176.92	105.64	1.15E-23			1	
H' <sub>All</sub>	<b>Full</b>	<b>437.26</b>	<b>0.00</b>	<b>1.00E+00</b>	A	N	6	0.37
	Climatic	575.97	138.71	7.58E-31			4	
	Density	489.62	52.36	4.27E-12			4	
	Null	623.24	185.98	4.12E-41			2	
H' <sub>WFleshy</sub>	<b>Climatic</b>	<b>380.50</b>	<b>0.00</b>	<b>1.00E+00</b>	A, R		6	0.16
	Density	423.01	42.51	5.87E-10			4	
	Null	422.19	41.69	8.85E-10			2	
H' <sub>WDry</sub>	<b>Full</b>	<b>467.26</b>	<b>0.00</b>	<b>1.00E+00</b>	A	N	6	0.31
	Climatic	569.08	101.82	7.76E-23			6	
	Density	518.07	50.81	9.26E-12			4	
	Null	625.44	158.19	4.48E-35			2	
H' <sub>Herbaceous</sub>	<b>Climatic</b>	<b>656.79</b>	<b>0.00</b>	<b>1.00E+00</b>	A, R		6	0.08
	Density	683.94	27.15	1.27E-06			4	
	Null	683.32	26.52	1.73E-06			2	

Notes: NP is the total number of parameters in the best model;  $\omega_i$  is the Akaike weight for each competing model; and  $R^2 = 1 - SSE/SST$  for the relationship between predicted and observed growth. The *Climatic axes* column indicates whether the best model incorporates terms for effects of altitude (A), annual radiation (R), or both. The  $\gamma$  column indicates whether (Y, yes; N, no) the best model also includes a term that allows sensitivity to pine density to vary with climatic conditions (either altitude [A] or annual radiation [R]).



## FIGURE CAPTIONS

FIG 1. Maps showing the situation of the study area (the Sierra Nevada mountains in southern Spain) and the location of the forest inventory plots (n = 442 for pine plantations, n = 45 for natural *Quercus ilex* forests, n = 26 for natural deciduous forests). All plots were situated within the Sierra Nevada National Park (highest level of protection), which is surrounded by an area of similar size (~86000 ha) protected as Natural Park.

FIG 2. Predicted variation in potential regeneration along gradients of a) altitude, b) annual radiation, c) stand density, and d) distance to the nearest *Quercus ilex* forest. See Appendix C for the estimated parameters of the corresponding functions. When the most parsimonious model allowed the stand density effect to vary as a function of climate, potential regeneration along the density gradient is represented at 1700 m a.s.l. of altitude and 5 GJ/m<sup>2</sup> of annual radiation (mean values for the data set).

FIG 3. Effect of climatic variables (altitude and annual radiation) on optimal stand densities for potential regeneration of a) *Quercus ilex* seedlings, b) *Quercus ilex* saplings, c) *Pinus nigra* seedlings, and d) *Pinus sylvestris* seedlings. Only those tree species for which the most parsimonious model included such an effect (Table 1) are represented. The arrows indicate the direction of displacement of optimal stand densities with increasing abiotic stress (i.e., lower altitude and higher radiation). See Appendix C for the estimated parameters of the corresponding Gaussian functions.

FIG 4. Effect of stand density on regeneration (seedlings/saplings per m<sup>2</sup>) at three different

altitudes: a) low = 1300 m, b) medium = 1700 m, and c) high = 2100 m. Low and high altitude represent the 10 and 90 quartiles of the distribution for all plantation plots. Regeneration values are calculated at mean radiation levels ( $5 \text{ GJ/m}^2$ ) and optimal dispersal distance (i.e., zero m from seed sources, the *distance effect* equals 1).

FIG 5. Predicted variation in potential richness (species number) and Shannon's ( $H'$ ) diversity index along gradients of altitude, annual radiation, and stand density. See Appendix D for the estimated parameters of the corresponding Gaussian functions.

FIG 6. Effect of stand density on richness (species number) and Shannon's ( $H'$ ) diversity index at different altitudinal levels (low = 1300 m, medium = 1700 m, high = 2100 m). Radiation was fixed at  $5 \text{ GJ/m}^2$ . Straight lines denote no effect of stand density on  $H'$  index values, and are included only for comparative purposes.

FIG 1.

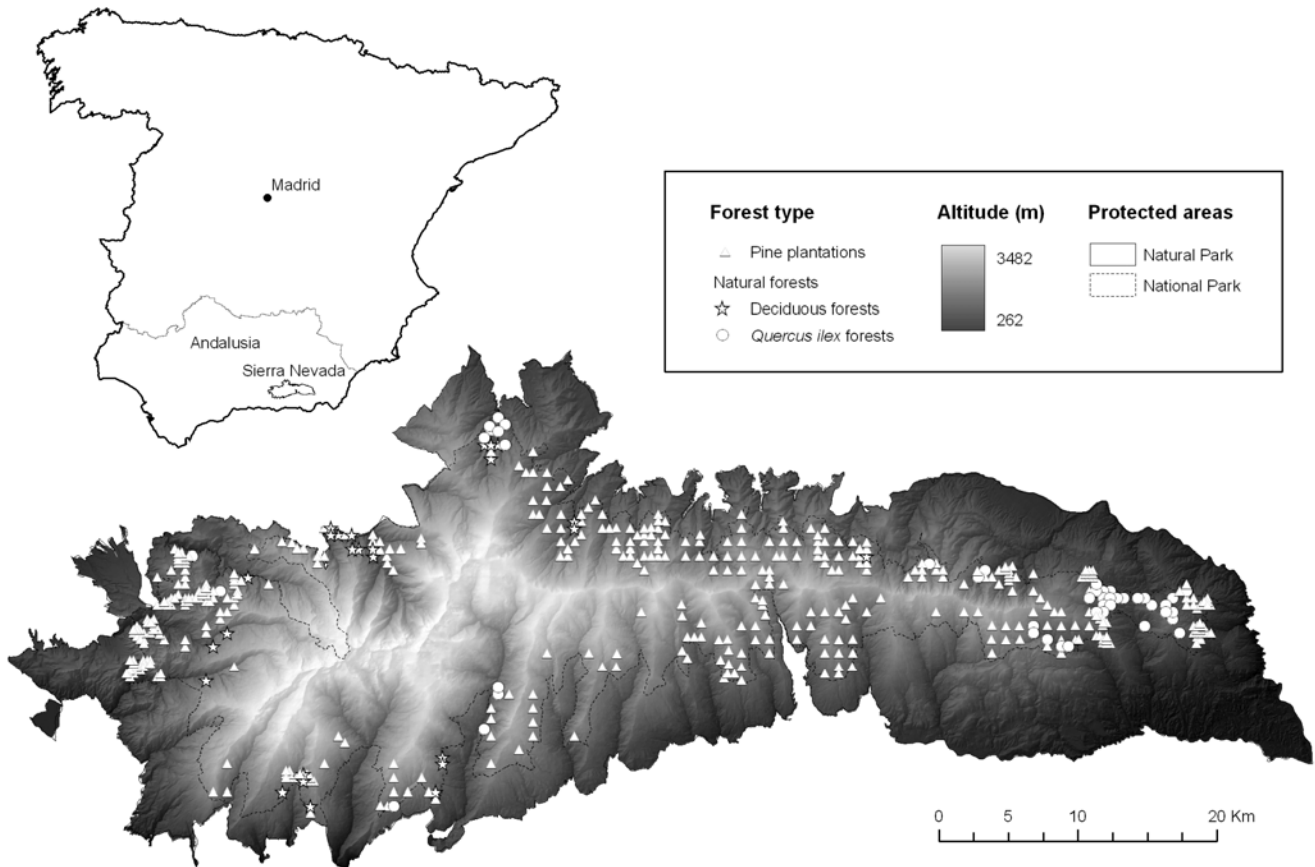


FIG 2.

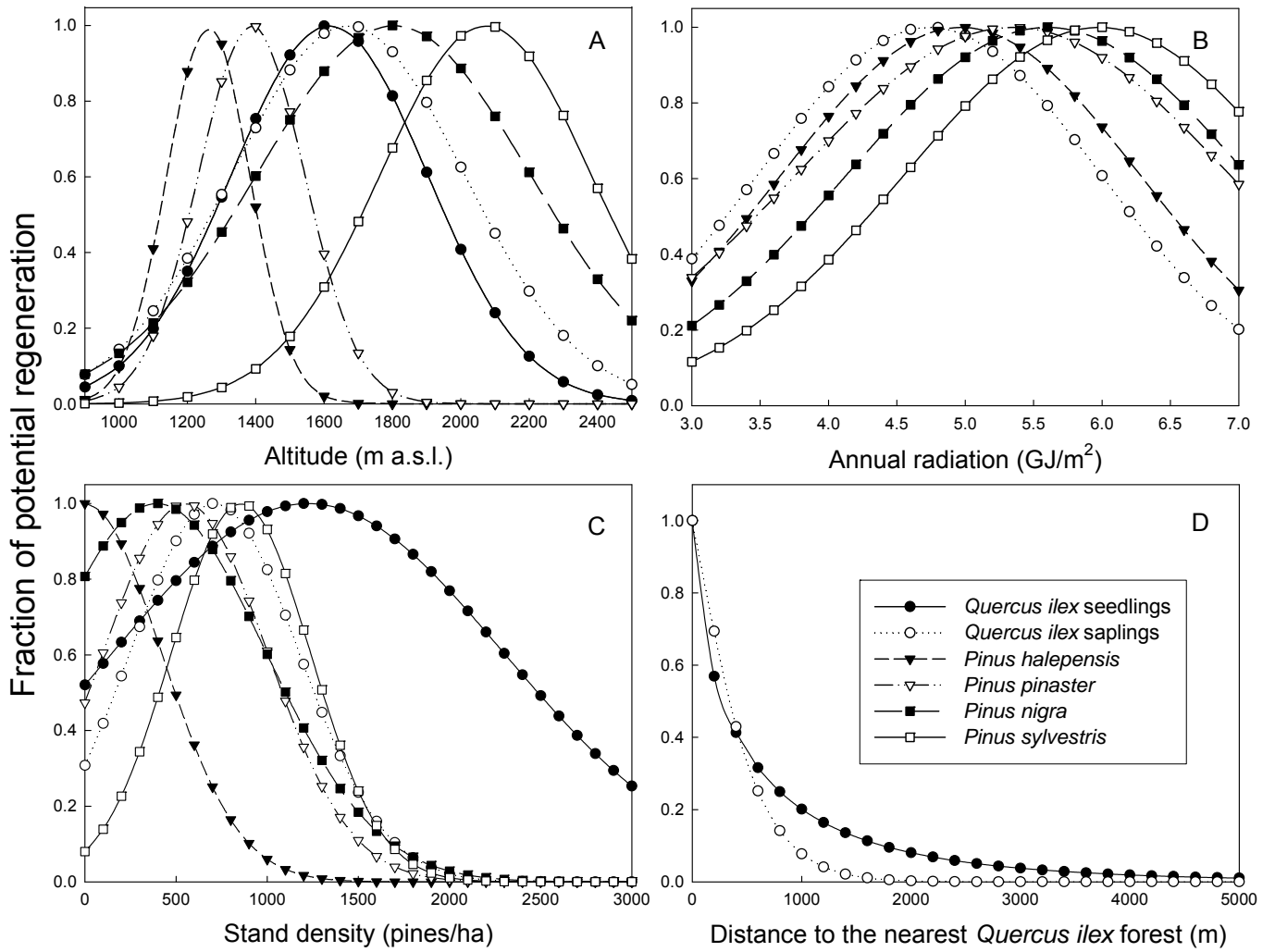


FIG 3.

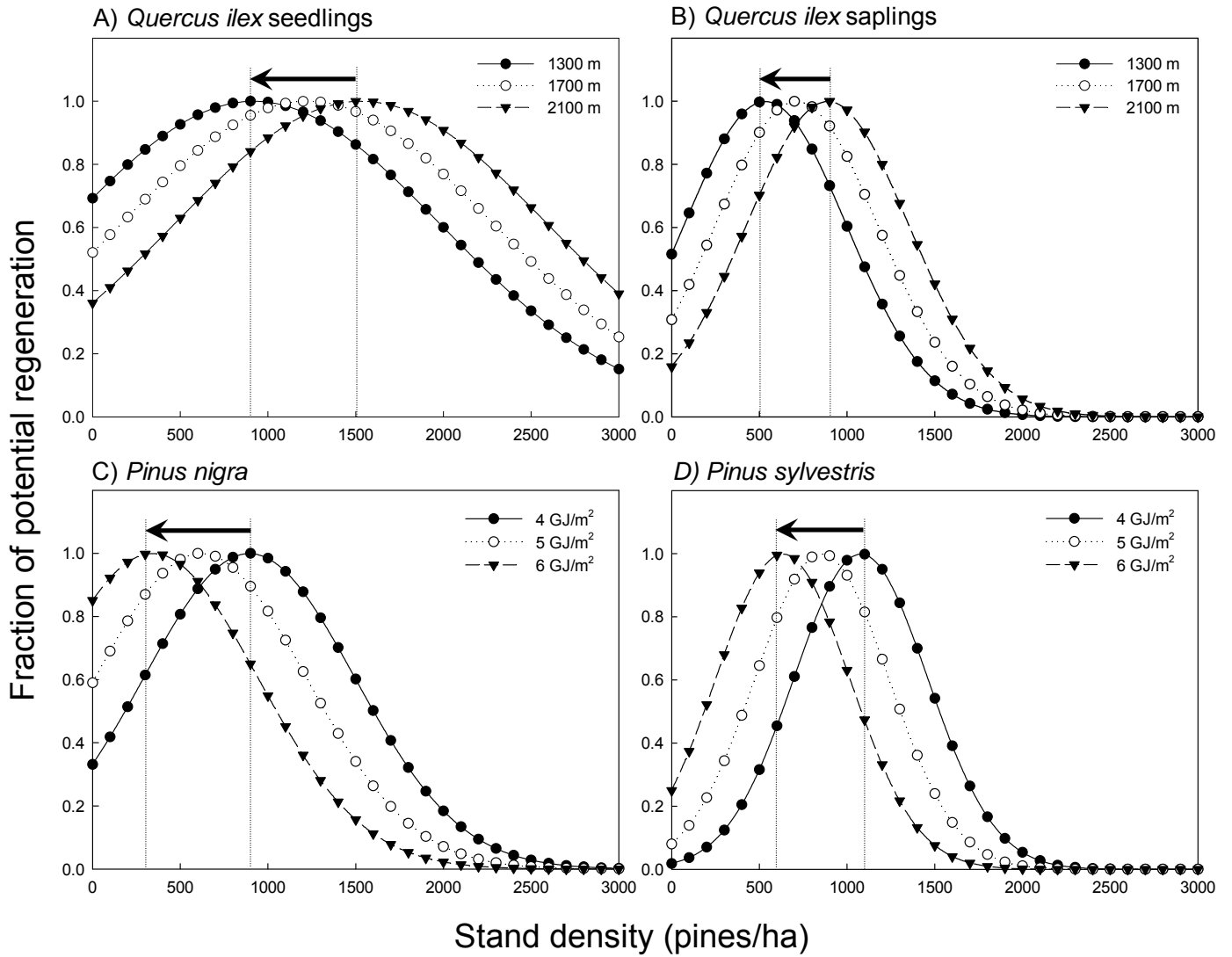


FIG 4.

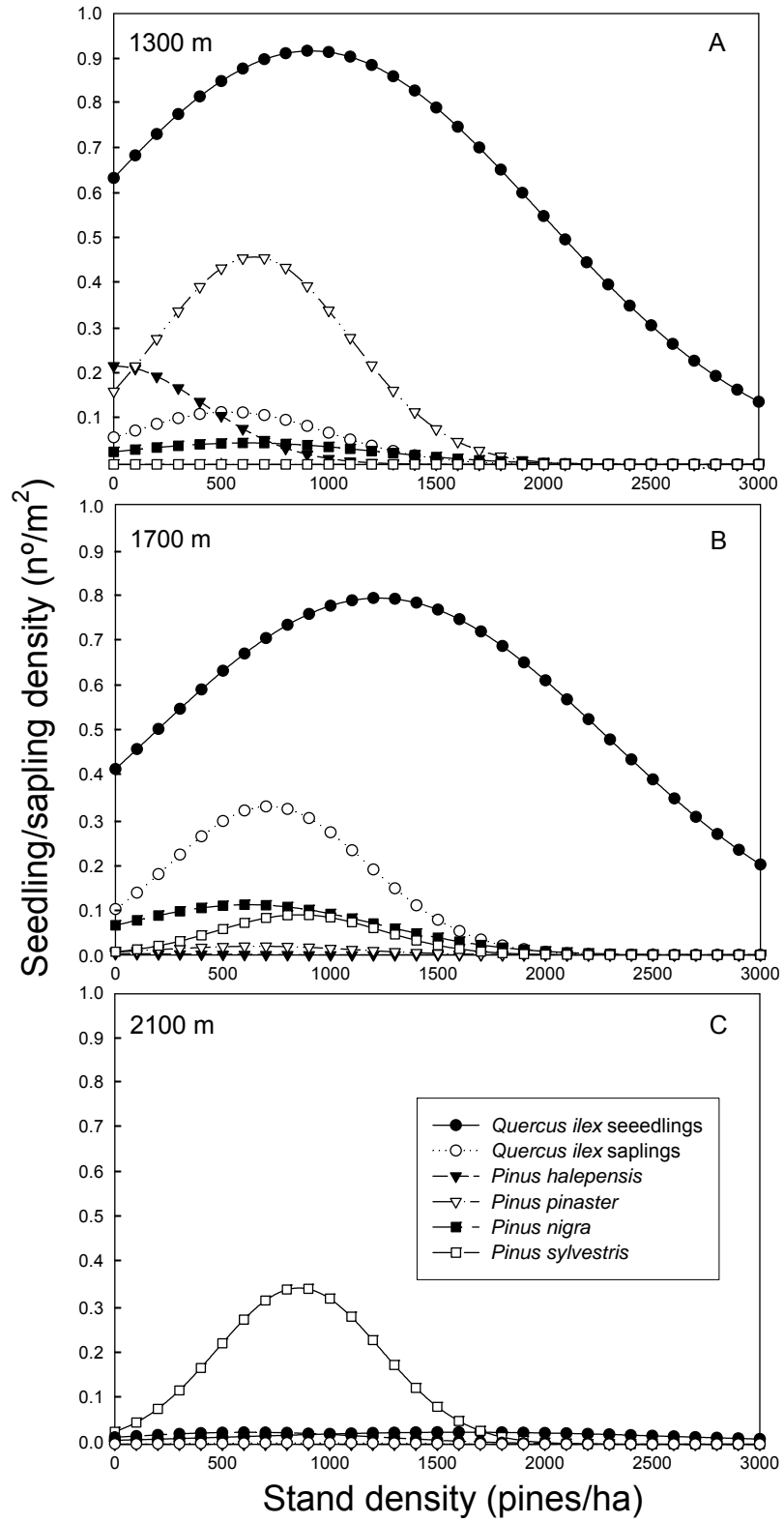


FIG 5.

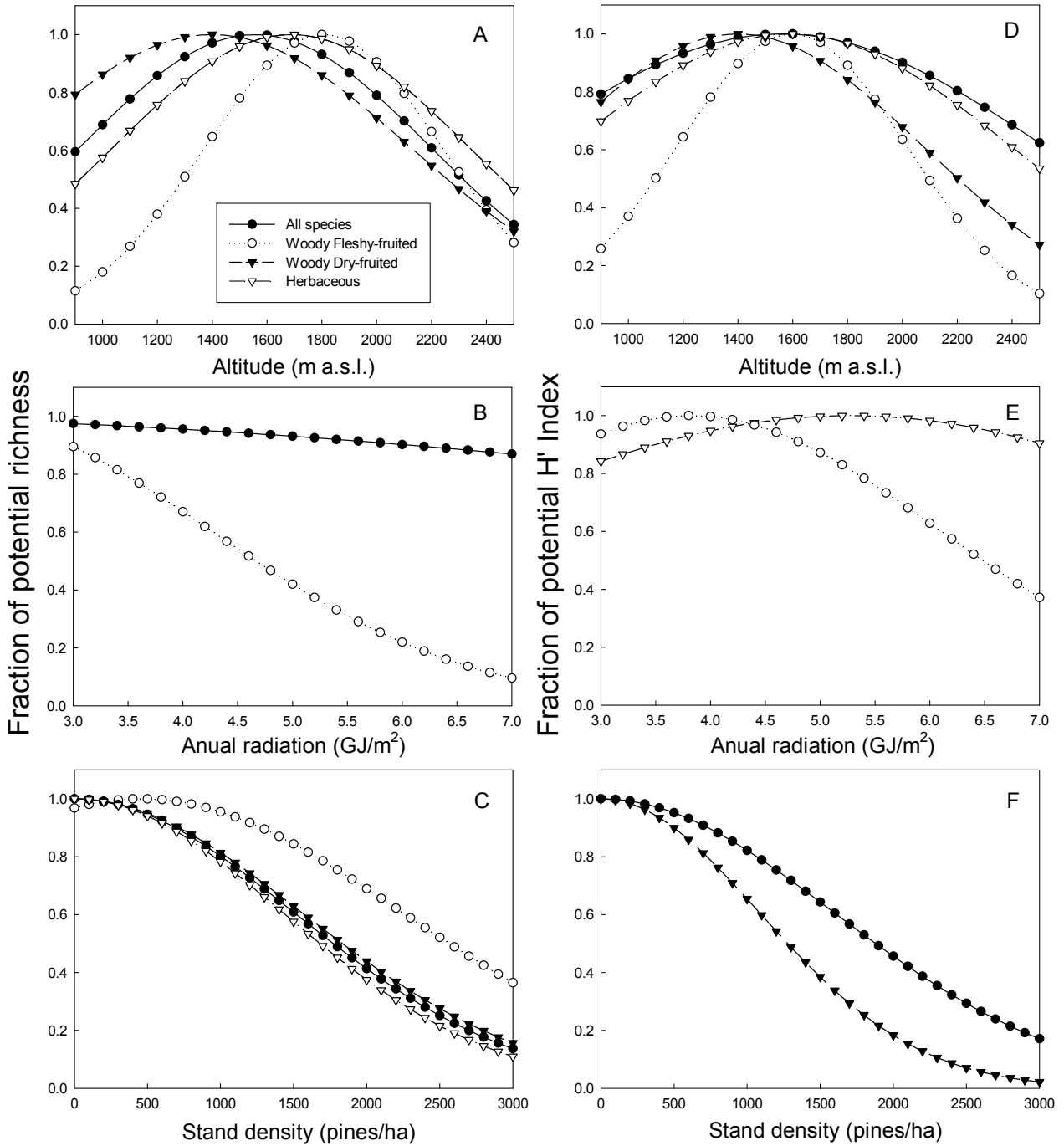


FIG 6.

