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Are pine plantations valid tools for restoring Mediterranean forests? An assessment along abiotic and biotic gradients

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

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

From a management perspective, different strategies will be necessary depending on where a plantation lies along the gradients explored. Active management will be required in high-density plantations with arrested succession and low diversity. Thinning could redirect plantations toward more natural densities where facilitation predominates. Passive management might be recommended for low- to moderate-density plantations with active successional dynamics (e.g., toward oak or pine–oak forests at low to mid altitudes). Enrichment planting will be required to overcome seed limitation, especially in plantations far from natural forests. We conclude that plantations should be perceived as dynamic systems where successional trajectories and diversity levels are determined by abiotic constraints, complex balances of competitive and facilitative interactions, the spatial configuration of native seed sources, and species life-history traits.

Key words: competition; environmental gradients; facilitation; management strategy; Mediterranean forests; pine plantations; regeneration; seed dispersal; Sierra Nevada National Park, Andalusia, southeast Spain; species diversity; stand density.

Introduction

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 2006). The area covered by forest plantations has increased dramatically in recent decades, currently representing approximately 140 million ha worldwide (FAO 2006). Although only 22% of this area has a primarily protective function (i.e., conservation of soil, water, and biodiversity), the importance of plantations in landscape management and restoration has

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increased recently, environmental protection being considered a legitimate objective even for productive plantations (Lamb 2005, Cummings and Reid 2008).

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

Discrepancies around the ecological consequences of forest plantations can arise, among other reasons, from the scarcity of studies that examine plantations along gradients of environmental conditions and stand characteristics. First, abiotic conditions (i.e., climatic characteristics, soil fertility) will influence the suitability of a plantation for natural regeneration and diversity recovery. For example, a few studies have shown that the suitability of pine plantations for woody species regeneration in Mediterranean areas is reduced in dry years and sites, presumably due to more intense competition for water (Maestre et al. 2004, Arrieta and Suárez 2006). Secondly, the stand structure of the plantation will influence the establishment of native species through biotic interactions such as competition (Grace and Tilman 2003) and facilitation (Callaway 2007). In this sense, the sign and magnitude of overstory–understory interactions might change as a function of overstory density (Thomas et al. 1999, Arévalo and Fernández-Palacios 2005, Paquette et al. 2006). However, the scarcity of studies that explore plantation effects along tree density gradients precludes identifying density thresholds that define the transition between negative and positive net effects on understory vegetation. Finally, in fragmented landscapes, dispersal distances and the frequency of long-distance dispersal events have a major influence on the probability of plant colonization and persistence in habitat patches (Cain et al. 2000, Pearson and Dawson 2005, Kunstler et al. 2007). Therefore, plantations close to seed sources could be expected to have more active recruitment and successional dynamics than plantations far from seed sources (Hewitt and Kellman 2002, White et al. 2004). In summary, the ecological consequences of a forest plantation will be largely influenced by its position along abiotic, biotic, and dispersal distance gradients.

In this study, we conduct a large-scale assessment of the ecological impacts of forest plantations in mountain landscapes of southern Spain. For this, we analyzed plant regeneration and diversity in 442 pine plantations plots covering a wide gradient of climatic conditions, stand density, and distance to natural forest fragments that act as seed sources. Plantations (mainly pines) cover millions of hectares in the Iberian Peninsula, as well as in most countries of the Mediterranean Basin, where they have been widely used to recover the forest surface area lost over thousands of years of human timber exploitation and conversion to agricultural lands (Pausas et al. 2004, FAO 2006). Fast-growing pines were considered an intermediate successional stage between the transitional shrubs and the mature tree community, and therefore assumed to facilitate the introduction of late-successional hardwoods (Barbéro et al. 1998, Pausas et al. 2004, Barčić et al. 2006). However, since most reforestation initiatives were not followed up with subsequent management or monitoring, it is unknown to what extent plantations successfully promote the recovery of native vegetation. Specifically, we ask: (1) What is, on average, the abundance of tree regeneration and the plant diversity of pine plantations, in comparison to native broadleaf forests? and (2) How does regeneration and diversity in plantations vary along gradients of climatic conditions, stand density, and distance to seed sources? The answers to these questions represent critical information to develop efficient strategies of plantation management that integrate the environmental heterogeneity found in the extensive areas covered by this type of novel ecosystem.

Material and Methods

Study site

The study was conducted at the Sierra Nevada National Park (Andalusia, southeast Spain; Fig. 1, Plate 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 above sea level (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. Additionally, the complex orography of the mountains causes strong climatic contrasts between the sunny and dry south-facing slopes and the shaded and wetter north-facing slopes.

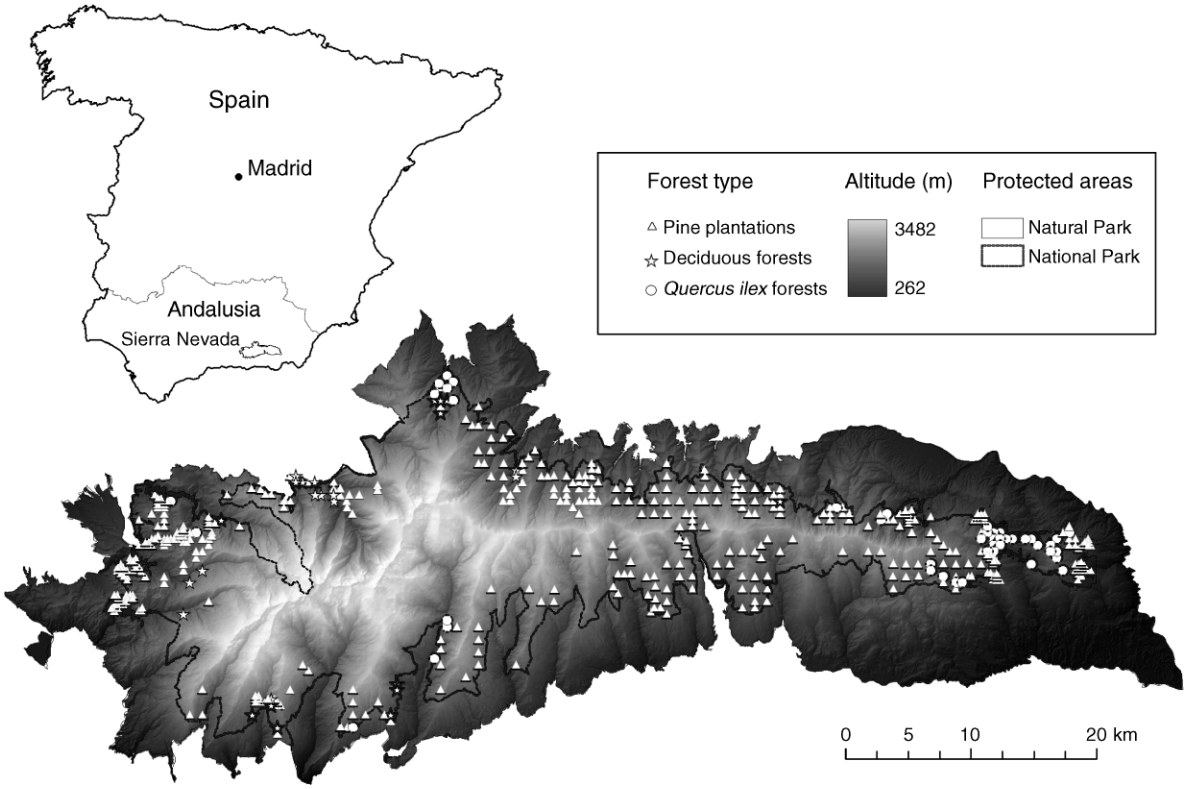

FIG. 1. Maps showing the situation of the study area (the Sierra Nevada mountains in southern Spain) and the location of the forest inventory plots ($n = 442$ for pine plantations, $n = 45$ for natural *Quercus ilex* forests, $n = 26$ for natural deciduous forests). All plots were situated within the Sierra Nevada National Park (highest level of protection), which is surrounded by an area of similar size (~86 000 ha) protected as Natural Park.

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

Data set

We analyzed 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 long-term permanent plots (20 × 20 m) distributed within the main forest units of the park: pine plantations, evergreen *Q. ilex* forests, and deciduous broadleaf forests. The network of plots is a random sample stratified by land cover and altitude, covering a gradient of 974–2439 m a.s.l. Within the 20 × 20 m plots, each live tree with a diameter at breast height (dbh) >7.5 cm was mapped, its species identity annotated and the dbh measured. Two additional circular subplots were established within each larger plot: a 5-m radius plot (78.5 m^2 in area) for the estimation of the number of seedlings (dbh < 2.5 cm and height < 1.3 m) and saplings (dbh = 2.5–7.5 cm) of tree species, and a 10-m radius plot (314 m^2 in area) for estimation of understory herbaceous and woody species composition and abundance. For resprouting species (i.e., *Quercus* spp.) our

approach does not allow a clear distinction between ramets and genets. This difficulty nevertheless did not significantly affect the main conclusions of the paper on regeneration patterns, which were based more on relative differences between natural forests and plantations, and among plantation plots, than on absolute numbers of recruits.

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

Each of the 442 plantation plots was characterized with 19 topographic and climatic variables. Raster maps and plot locations (UTM coordinates) were combined to determine the values of each abiotic variable in each plot using ArcView Gis 9.2 (ESRI Inc., Redlands, California, USA). The 19 abiotic variables were altitude (determined from a digital elevation model with a 10-m resolution); annual and seasonal (i.e., spring, summer, fall, and winter) precipitation (from Sánchez et al. 1999); annual mean, maximum, and minimum temperature (from Sánchez et al. 1999); annual and seasonal (i.e., spring, summer, fall, and winter) radiation (obtained from a digital elevation model with a 10-m resolution); annual potential evapotranspiration, measured as a function of mean temperature (Thornthwaite 1948); annual water deficit, calculated as the sum of negative differences between annual precipitation and potential evapotranspiration; annual water surplus, calculated as the sum of positive differences between annual precipitation and potential evapotranspiration; drought length, taken as the number of months in which potential evapotranspiration exceeded precipitation; and weeks with snow, calculated as the average number of weeks with snow per year (period 2001–2007) using the normalized difference snow index (NDSI) from MODIS images (Salomonson and Appel 2004). The relationship among the 19 abiotic variables were explored with principal component analyses (PCA). The first axis of the PCA (explaining 67.7% of the variance) was strongly correlated with altitude, precipitation, temperature, and drought indices. The second axis (explaining 15.6% of the variance) was strongly correlated with radiation variables. Therefore, we chose for our modeling analyses two variables representative of each of the two axes: altitude and annual radiation. Altitude summarizes the simultaneous variation in precipitation and temperature associated with altitudinal gradients in mountain areas, whereas annual radiation summarizes the variation in solar irradiance that occurs due to variations in slope (higher radiation at low slopes), aspect (higher radiation in southern orientations) and altitude (higher radiations at high altitudes). We considered these two variables to represent a synthesis of the complex climatic regimes of the Sierra Nevada Mountains.

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

A maximum likelihood analyses of regeneration and diversity

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

Regeneration models.—We conducted separate analyses of seedling density (i.e., number of seedlings [dbh < 2.5 cm and height < 1.3 m] in the 5 m radius subplots) for the five most common tree species (*Q. ilex*, *P. halepensis*, *P. pinaster*, *P. nigra*, and *P. sylvestris*). These species comprised 94.3% of the total number of seedlings found in the 442 plantation plots ($n = 4215$ seedlings). Seedlings of deciduous native tree species were not analyzed due to insufficient number. We also conducted an additional analysis for the density of *Q. ilex* saplings (dbh = 2.5–7.5 cm). This analysis was not conducted for pine saplings because we could not distinguish which of these small pines were natural recruits and which were suppressed adult planted pines. In fact, most pine saplings appeared in plantations with extremely high (>2000 pines/ha) canopy densities.

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

to seed sources equaled zero in all cases). Our full model has the following form:

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

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

$$\text{Climatic effect} = \exp\left[-\frac{1}{2}\left(\frac{\text{Altitude} - \text{XA}_0}{\text{XA}_b}\right)^2\right] \times \exp\left[-\frac{1}{2}\left(\frac{\text{Radiation} - \text{XR}_0}{\text{XR}_b}\right)^2\right] \quad (2)$$

where XA_0 and XR_0 are the altitude and annual radiation values, respectively, at which maximum potential seedling/sapling number occurs; and XA_b and XR_b are estimated parameters that control the breadth of the function (i.e., the variance of the normal distribution). Eq. 2 produces the classic Gaussian distribution of species performance along an environmental axis usually assumed to describe vegetation–environment relationships (e.g., Curtis 1959, Whittaker 1975, Gauch 1982), but can also produce sigmoidal, monotonic curves within restricted ranges of either axis. We also tested univariate functions in which terms for one of the two axes were dropped from the analysis.

The density effect was modeled using a univariate Gaussian function:

$$\text{Density effect} = \exp\left[-\frac{1}{2}\left(\frac{\text{Density} - \text{XD}_0}{\text{XD}_b}\right)^2\right] \quad (3)$$

where XD_0 represents the pine density (pines/ha) at which maximum seedling/sapling density occurs, and XD_b controls the breadth of the function. The density effect was also tested using pine basal area instead of density as predictor, but in no case were the models a better fit (data not shown).

We also tested a variant of Eq. 3 in which the density effect was allowed to vary as a function of the climatic conditions of the plot. This effect is independent of the underlying direct effect of climate on potential regeneration (i.e., the climatic effect). For this, the mode term (XD_0) in Eq. 3 was allowed to vary as a function of climatic variables (either altitude or annual radiation):

$$\text{XD}_0 = \text{XD}_0 + \gamma \times \text{Climatic variable}. \quad (4)$$

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

We tested two alternative forms to model the distance effect: a Weibull dispersal function (the most used in previous studies; see Ribbens et al. 1994, Clark et al. 1998, LePage et al. 2000) and a lognormal dispersal function (suggested by Greene et al. 2004 to fit empirical data as well as or better than Weibull functions). However, because the lognormal function was in no case a better fit to the data than the Weibull function (results not shown for simplicity), we selected the Weibull dispersal kernel to model the distance effect. The Weibull function has the form

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

where α controls the rate of decrease of seedling/sapling density with distance, and β controls the shape of the function.

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

Parameter estimation, model comparison, and model evaluation

We first compared evidence for each of the three independent factors (climate, stand density, distance to seed sources) separately by comparing the Akaike information criterion (AIC) of their regression models to the AIC of the value of a null model (i.e., mean or intercept-only model). Null models were also run for total regeneration (i.e., number of seedlings/saplings of all tree species together) in both plantation and natural forest plots, as well as for richness and H' index in natural forest plots, in order to compare mean values of natural regeneration and diversity in pine plantations vs.

natural broadleaf forests. We then tested increasingly complex models by combining sets of independent factors for which there was evidence (as measured by AIC) of univariate effects. The absolute magnitude of the differences in AIC between alternate models (ΔAIC) provides an objective measure of the strength of empirical support for the competing models. ΔAIC values were also used to derive the Akaike weights (w_i) for the set of candidate models (Burnham and Anderson 2002). The Akaike weight of model i can be interpreted as the expected probability of that model being selected as best when repeated independent samples are taken from the same population. The best model is considered to be clearly superior to the other candidate models when its $w_i \geq 0.9$.

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

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

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

We used simulated annealing, a global optimization procedure, to determine the most likely parameters (i.e., the parameters that maximize the log-likelihood) given our observed data (Goffe et al. 1994). The R^2 of the regression (1 − SSE/SST) of observed vs. predicted values was used as a measure of goodness of fit (SSE, sum of squares error; SST, sum of squares total). We used asymptotic two-unit support intervals to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards 1992). A support interval is defined as the range of the parameter value that results in less than a two-unit difference in AIC. It is roughly equivalent to a 95% support limit defined using a likelihood ratio test (Hilborn and Mangel 1997). All analyses were performed using R v 2.5.0 (R Development Core Team 2006) and the *likelihood* package v 1.1 (*available online*).[6]

Results

Regeneration

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

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

Seedling species also segregated along a gradient of stand density: *P. halepensis* reached maximum seedling densities at low values of pine density (0–100 pines/ha), tending to null regeneration within 1000–1500 pines/ha (Fig. 2C; Appendix C). The three remaining pine species and *Q. ilex* saplings had recruitment peaks (XD_0 parameter) at densities between 400 and 900 pines/ha, tending to null regeneration within 1500–2000 pines/ha. Finally, *Q. ilex* seedling abundance peaked at 1100–1300 pines/ha, some seedlings recruiting at even 3000 pines/ha. Moreover, for three of the five tree species, our data supported a model in which the mode of the density effect was allowed to vary as a function of the climatic

[6] ⟨http://www.ecostudies.org/lme_R_code_tutorials.html⟩

TABLE 1. Comparison of the alternate models of regeneration (i.e., seedling and sapling density) for the five most common tree species in plantation understories ($n = 442$ plots).

Species and model	AIC_c	ΔAIC_c	ω_i	Climatic axes	γ	NP	R^2
$QUIL_{SDL}$							
Full	**3841.05**	**0.00**	**1.00**	A	Y [A]	11	0.25
Density + Climatic	4151.06	310.01	4.81×10^{-68}			9	
Dispersal + Climatic	4074.43	233.38	2.10×10^{-51}			8	
Dispersal + Density	4246.81	405.76	7.77×10^{-89}			7	
Climatic	4257.60	416.55	3.53×10^{-91}			6	
Density	4860.90	1019.85	3.49×10^{-222}			4	
Dispersal	4419.10	578.05	3.01×10^{-126}			4	
Null	5020.09	1179.04	9.43×10^{-257}			2	
$QUIL_{SAP}$							
Full	**437.14**	**0.00**	$\mathbf{9.04 \times 10^{-1}}$	A, R	Y [A]	11	0.20
Density + Climatic	444.19	7.05	2.66×10^{-2}			9	
Dispersal + Climatic	442.32	5.18	6.78×10^{-2}			8	
Dispersal + Density	451.02	13.88	8.75×10^{-4}			7	
Climatic	452.16	15.02	4.95×10^{-4}			6	
Density	475.06	37.92	5.27×10^{-9}			4	
Dispersal	454.70	17.56	1.39×10^{-4}			4	
Null	486.74	49.60	1.53×10^{-11}			2	
$PIHA_{SDL}$							
Full	**301.54**	**0.00**	**1.00**	A, R	N	8	0.30
Climatic	358.68	57.14	3.91×10^{-13}			6	
Density	362.98	61.44	4.55×10^{-14}			4	
Null	394.51	92.97	6.48×10^{-21}			2	
$PIPI_{SDL}$							
Full	**963.20**	**0.00**	**1.00**	A, R	N	8	0.37
Climatic	1074.45	111.3	6.96×10^{-25}			6	
Density	1136.32	173.1	2.56×10^{-38}			4	
Null	1408.12	444.9	2.44×10^{-97}			2	
$PINI_{SDL}$							
Full	**238.45**	**0.00**	**1.00**	A, R	Y [R]	9	0.79
Climatic	271.34	32.89	7.21×10^{-8}			6	
Density	343.91	105.46	1.26×10^{-23}			4	
Null	376.41	137.96	1.10×10^{-30}			2	
$PISI_{SDL}$							
Full	**808.86**	**0.00**	**1.00**	A, R	Y [R]	9	0.48
Climatic	952.97	144.11	5.09×10^{-32}			6	
Density	1068.00	259.14	5.35×10^{-57}			4	
Null	1169.99	361.13	3.82×10^{-79}			2	

Notes: NP is the total number of parameters in the best model; ω_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 γ 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]). Abbreviations are: $QUIL_{SDL}$, *Quercus ilex* seedlings; $QUIL_{SAP}$, *Q. ilex* saplings; $PIHA_{SDL}$, *Pinus 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.

conditions of the plot (Table 1). Thus, for *Q. ilex* seedlings and saplings, the maximum seedling abundance occurred at lower pine densities with decreasing altitude (i.e., decreasing precipitation and increasing temperature, positive values of the γ parameter; Fig. 3A, B and Appendix C). For *P. nigra* and *P. sylvestris*, the maximum seedling abundance occurred at lower pine densities with increasing annual radiation (negative values of the γ parameter; Fig. 3C, D).

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

Altogether, the effects of climate, stand density, and dispersal distance determined that plantations at low (~1300 m a.s.l.) and middle altitudes (~1700 m a.s.l.) and with moderate stand densities (500–1000 pines/ha) had the highest seedling and sapling abundance, mainly of *Q. ilex*, but also of the four pine species (Fig. 4A, B).

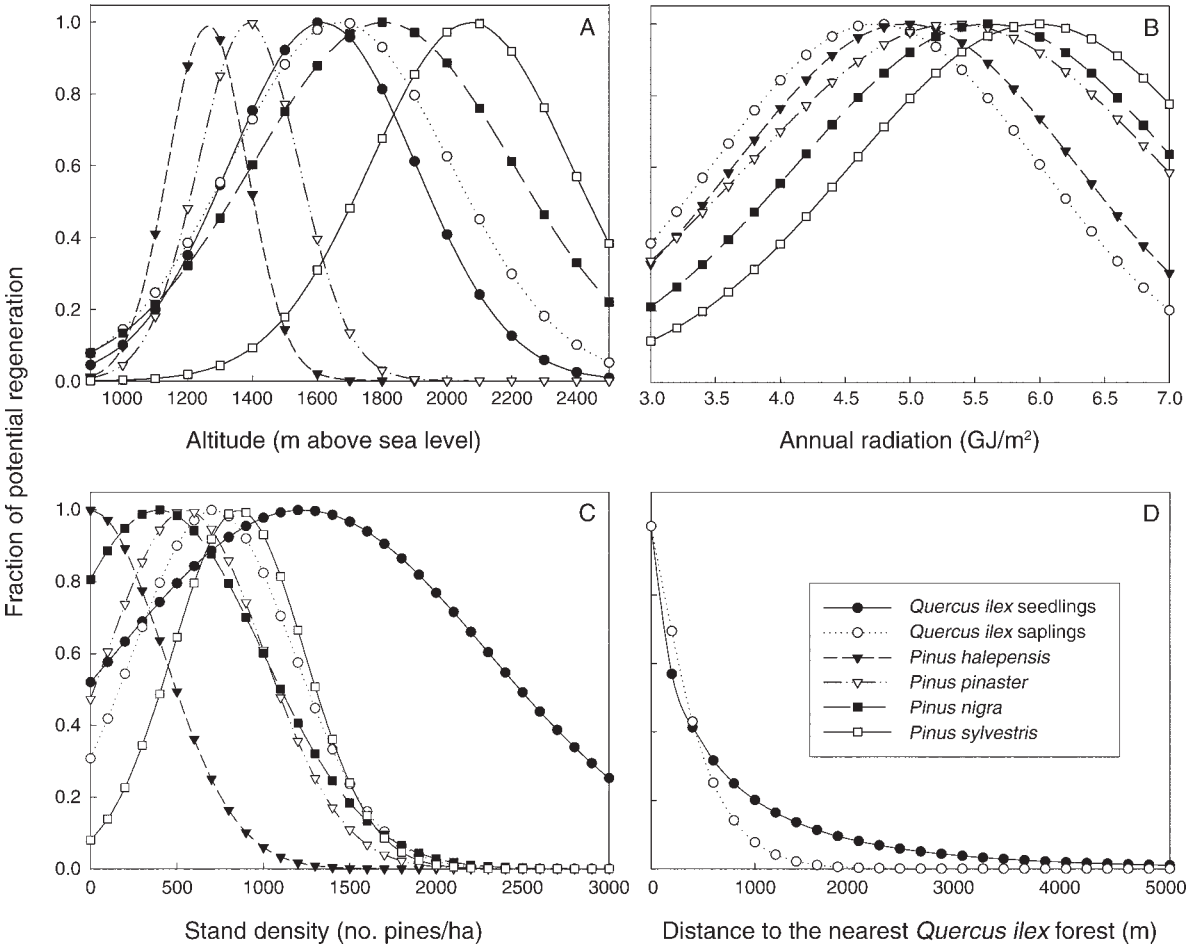

FIG. 2. Predicted variation in potential regeneration along gradients of (A) altitude, (B) annual radiation, (C) stand density, and (D) distance to the nearest *Quercus ilex* forest. See Appendix C for the estimated parameters of the corresponding functions. When the most parsimonious model allowed the stand density effect to vary as a function of climate, potential regeneration along the density gradient was represented at 1700 m above sea level of altitude and 5 GJ/m^2 of annual radiation (mean values for the data set).

At these altitudinal levels, even the densest plantations had some regeneration thanks to the capacity of *Q. ilex* to recruit at even 3000 pines/ha. On the contrary, high-altitude plantations (~2100 m a.s.l.) had much lower recruitment, the seedling bank being largely dominated by *P. sylvestris* (Fig. 4C). At this altitude, plantations with >2000 pines/ha were totally devoid of regeneration.

Diversity

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

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

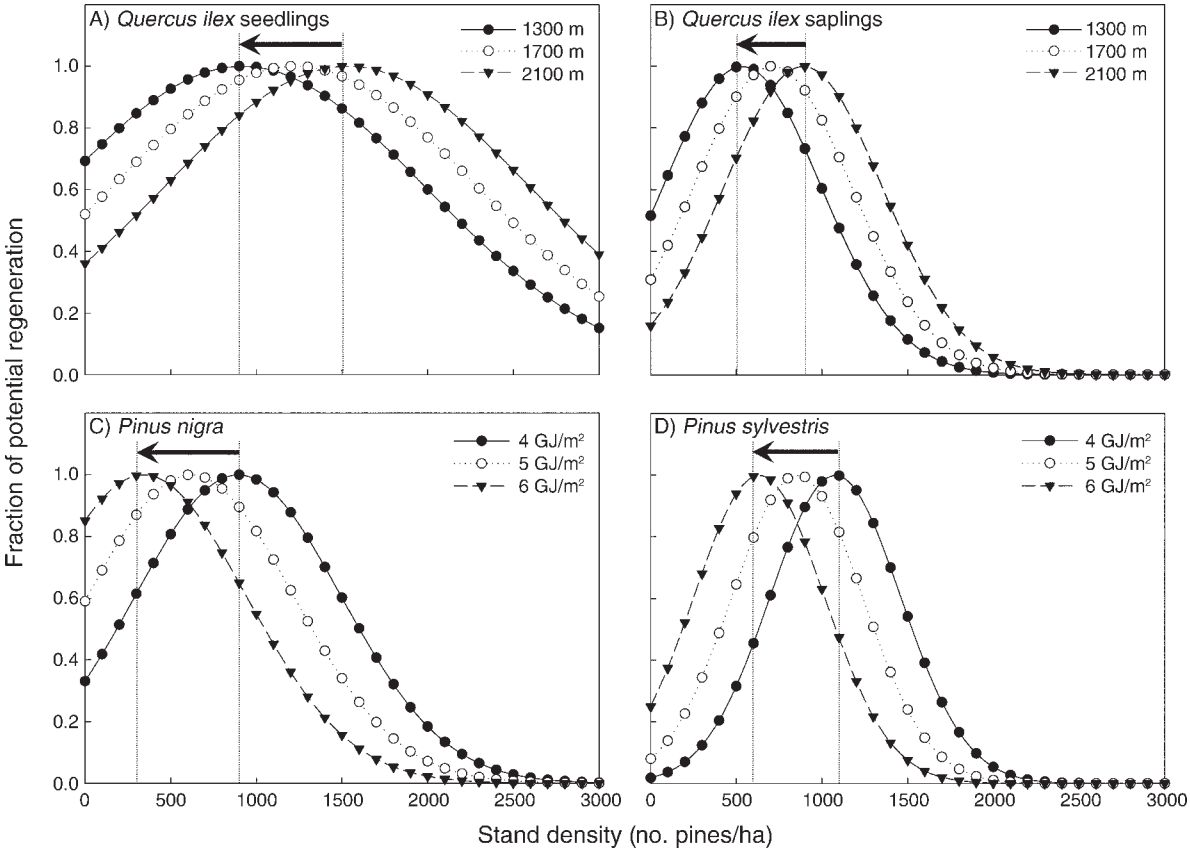

FIG. 3. Effect of climatic variables (three levels of altitude and three levels of annual radiation) on optimal stand densities for potential regeneration of (A) *Quercus ilex* seedlings, (B) *Quercus ilex* saplings, (C) *Pinus nigra* seedlings, and (D) *Pinus sylvestris* seedlings. Only those tree species 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.

curves of dry-fruited woody and herbaceous species peaked at zero density values, maximum richness of fleshy-fruited woody species occurred at a greater density (XD_0 = 455.78 pines/ha; Appendix D) and decreased at a slower rate (larger XD_b parameter) with increasing density (Fig. 5C).

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

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

DISCUSSION

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

Effects of pine plantations on tree regeneration

We developed models that relate the seedling and sapling density of the most common tree species in plantation understories with the abiotic (climate, distance to seed sources) and biotic (stand density) characteristics of the plantation plots. For the five species tested, we found strong empirical support ($w_i >$ 0.9) for the full model that included all these factors as predictors of regeneration. Tree seedling density varied along the three gradients from virtually zero to values close to those found in natural forests of Sierra Nevada (~1 seedling/m^2; Fig. 4). Therefore, regeneration dynamics in a particular plantation were highly dependent on the specific characteristics of the plot.

Plantations at low to mid altitudes had a more diverse and abundant seedling and sapling bank than high-altitude plantations (Fig. 4). The former showed a seedling bank dominated by *Q. ilex* and accompanied by several pine species (*P. halapensis*, *P. pinaster*, *P. nigra*), whereas the latter showed a virtually monospecific seedling bank of *P. sylvestris*. The fact that *P. sylvestris* had maximum seedling density at higher altitude than the other tree species is consistent with its domination of the tree line in Sierra Nevada, where extremely low temperatures and high radiation can limit the establishment of other pine and *Quercus* species. Based on the species composition of the seedling bank, high-mountain plantations could be expected to exhibit autosuccessional dynamics and perpetuate as monospecific *P. sylvestris* plantations. On the contrary, low- to medium-altitude plantations could be expected to follow a successional trajectory towards the replacement of pine forests by oak or mixed pine–oak forests, as suggested by the much larger seedling numbers of *Q. ilex* than of any pine species. This pine–oak replacement is in agreement with previous studies conducted in Mediterranean areas (Retana et al. 1999, Lookingbill and Zavala 2000) and other parts of the world where pines and oaks are also major structural components of forest ecosystems (Zavala et al. 2007).

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

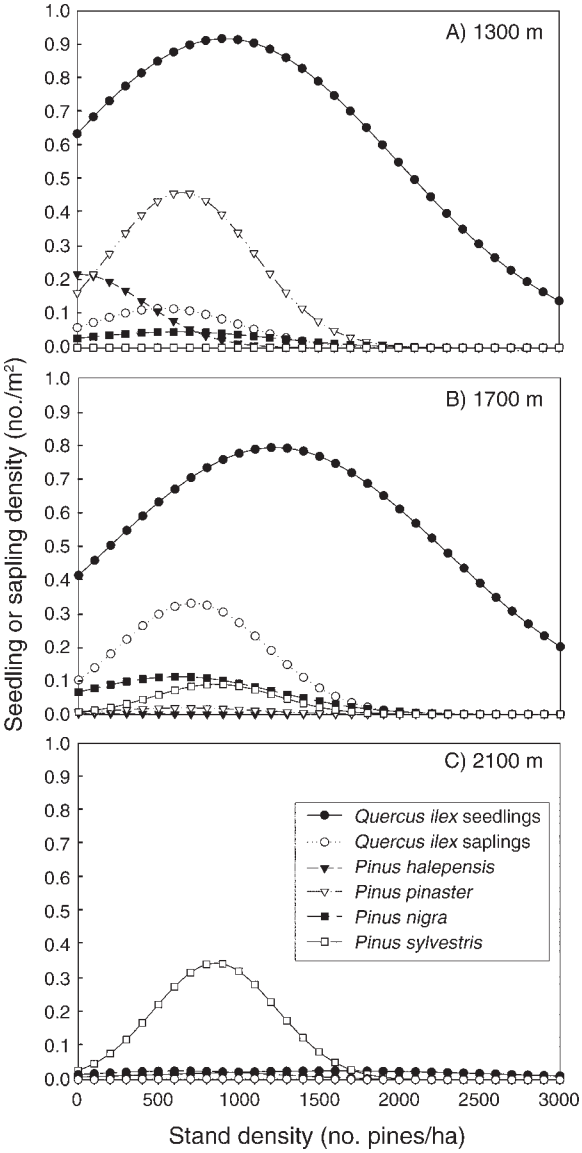

FIG. 4. Effect of stand density on regeneration (seedlings or saplings per m^2) at three different altitudes: (A) low = 1300 m, (B) medium = 1700 m, and (C) high = 2100 m. Low and high altitude represent the 10th and 90th quartiles of the distribution for all plantation plots. Regeneration values are calculated at mean radiation levels (5 GJ/m^2) and optimal dispersal distance (i.e., 0 m from seed sources; the distance effect equals 1).

TABLE 2. Comparison of the alternate models of species richness and biodiversity (Shannon's index, H') in plantation understories ($n = 442$ plots).

Variable and model	AIC_c	ΔAIC_c	ω_i	Climatic axes	γ	NP	R^2
$Richness_{All}$							
Full	**2675.23**	**0.00**	**1.00**	A, R	N	7	0.36
Climatic	2869.33	194.10	7.11×10^{-43}			5	
Density	2848.58	173.35	2.28×10^{-38}			3	
Null	3091.04	415.81	5.11×10^{-91}			1	
$Richness_{WFleshy}$							
Full	**1489.24**	**0.00**	$\mathbf{9.84 \times 10^{-1}}$	A, R	N	7	0.31
Climatic	1497.44	8.21	1.63×10^{-2}			5	
Density	1774.51	285.27	1.11×10^{-62}			3	
Null	1810.92	321.68	1.38×10^{-70}			1	
$Richness_{WDry}$							
Full	**2106.08**	**0.00**	**1.00**	A	N	6	0.31
Climatic	2216.58	110.51	1.01×10^{-24}			3	
Density	2178.37	72.29	2.01×10^{-16}			3	
Null	2582.01	475.93	4.50×10^{-104}			1	
$Richness_{Herbaceous}$							
Full	**2071.28**	**0.00**	**1.00**	A	N	6	0.14
Climatic	2147.83	76.55	2.38×10^{-17}			3	
Density	2105.16	33.88	4.40×10^{-8}			3	
Null	2176.92	105.64	1.15×10^{-23}			1	
H'_{All}							
Full	**437.26**	**0.00**	**1.00**	A	N	6	0.37
Climatic	575.97	138.71	7.58×10^{-31}			4	
Density	489.62	52.36	4.27×10^{-12}			4	
Null	623.24	185.98	4.12×10^{-41}			2	
$H'_{WFleshy}$							
Climatic	**380.50**	**0.00**	**1.00**	A, R		6	0.16
Density	423.01	42.51	5.87×10^{-10}			4	
Null	422.19	41.69	8.85×10^{-10}			2	
H'_{WDry}							
Full	**467.26**	**0.00**	**1.00**	A	N	6	0.31
Climatic	569.08	101.82	7.76×10^{-23}			6	
Density	518.07	50.81	9.26×10^{-12}			4	
Null	625.44	158.19	4.48×10^{-35}			2	
$H'_{Herbaceous}$							
Climatic	**656.79**	**0.00**	**1.00**	A, R		6	0.08
Density	683.94	27.15	1.27×10^{-6}			4	
Null	683.32	26.52	1.73×10^{-6}			2	

Notes: NP is the total number of parameters in the best model; ω_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 γ 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]). 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.

Pugnaire 2006, Gómez-Aparicio 2008). *Pinus halepensis* was the only tree species that did not benefit from a moderate pine density. This result agrees with the fact that this species is considered the most drought-tolerant pine in the Mediterranean basin (Barberó et al. 1998), and that facilitation by neighbors is usually more common in stress-intolerant than in stress-tolerant species (Liancourt et al. 2005, Michalet et al. 2006, Gómez-Aparicio et al. 2008). Overall, our analyses reveal regeneration patterns that are consistent with a shift from facilitation to competition in the overstory–understory interaction along the stand density gradient. Therefore, the rationale behind the establishment of pine plantations in degraded Mediterranean systems, its nurse role of native vegetation, applies only over a relatively small fraction (<1000 pines/ha) of the entire density gradient found at the landscape scale.

It bears noting that we found support for the shift between facilitation and competition occurring at different stand density thresholds depending on local climate (Fig. 3). Thus, maximum recruitment of *Q. ilex* and mountain pines (*P. nigra* and *P. sylvestris*) occurred at lower stand densities with decreasing altitude (i.e., decreasing precipitation and increasing temperature) or increasing radiation. This result suggests that, under stressful conditions of low water availability (i.e., low altitude and high radiation) the potential benefits of the pine overstory (e.g., amelioration of extreme climatic

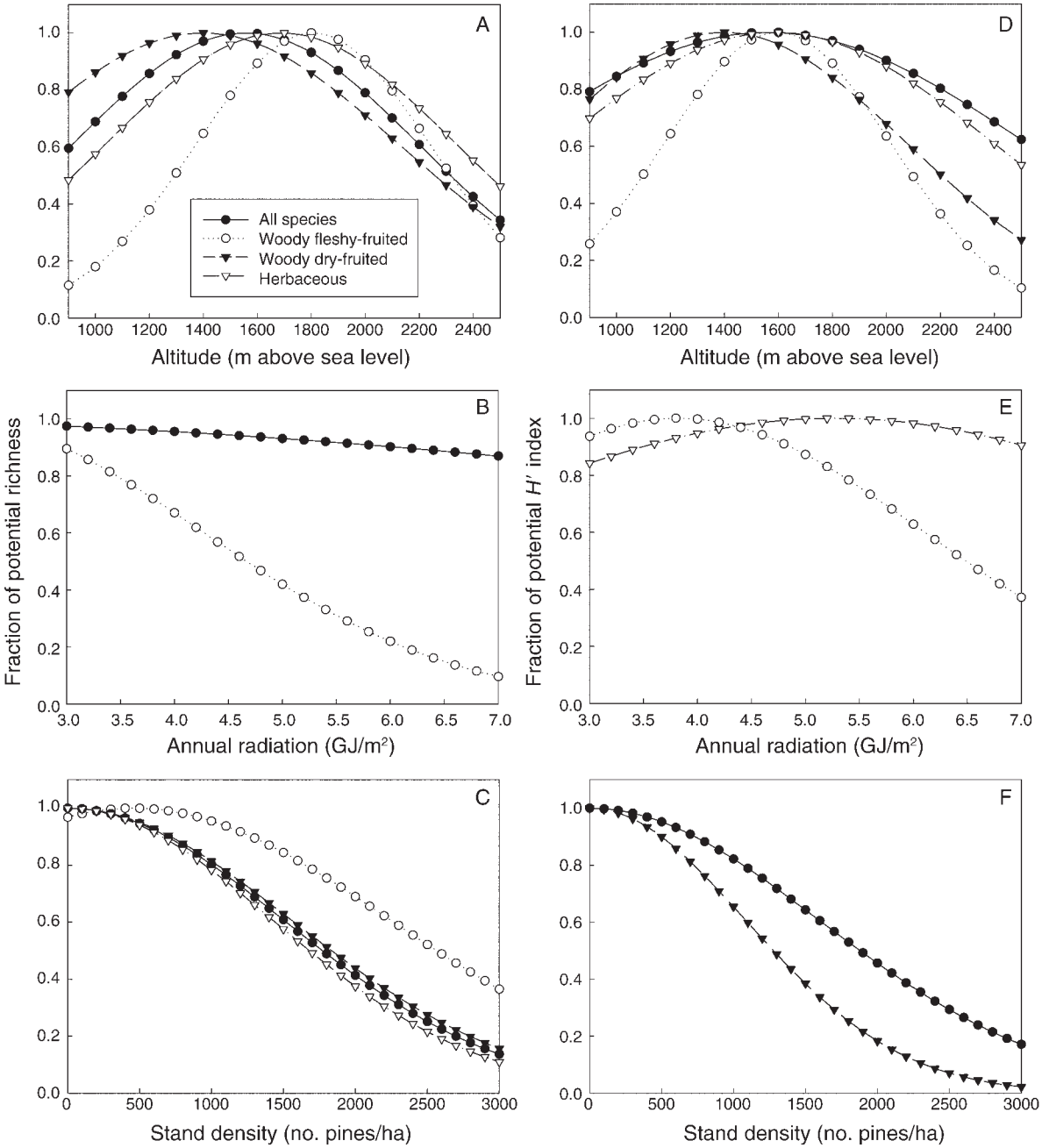

FIG. 5. Predicted variation in potential richness (species number) and Shannon's (H') diversity index along gradients of altitude, annual radiation, and stand density. See Appendix D for the estimated parameters of the corresponding Gaussian functions.

conditions) are quickly outweighed by the negative effects of competition for water. In fact, pine plantations have been shown to have a strong desiccating effect on soils due to high rainfall interception and water uptake (Maestre et al. 2003, Bellot et al. 2004, Farley et al. 2005). However, when water availability increases (i.e., high altitude and low radiation) competition for water relaxes, the shift from facilitation to competition occurs at higher stand densities, and net facilitation is found over a larger fraction of the density gradient. This line of reasoning is also supported by the fact that *P. halepensis* and *P. pinaster* (the two most drought-tolerant pines) were the only seedling species for which optimal stand density did not vary with climate, probably due to their higher ability to tolerate the negative effects of competition for water with canopy trees. The verification of this mechanistic explanation requires, however, an experimental study analyzing how soil characteristics,

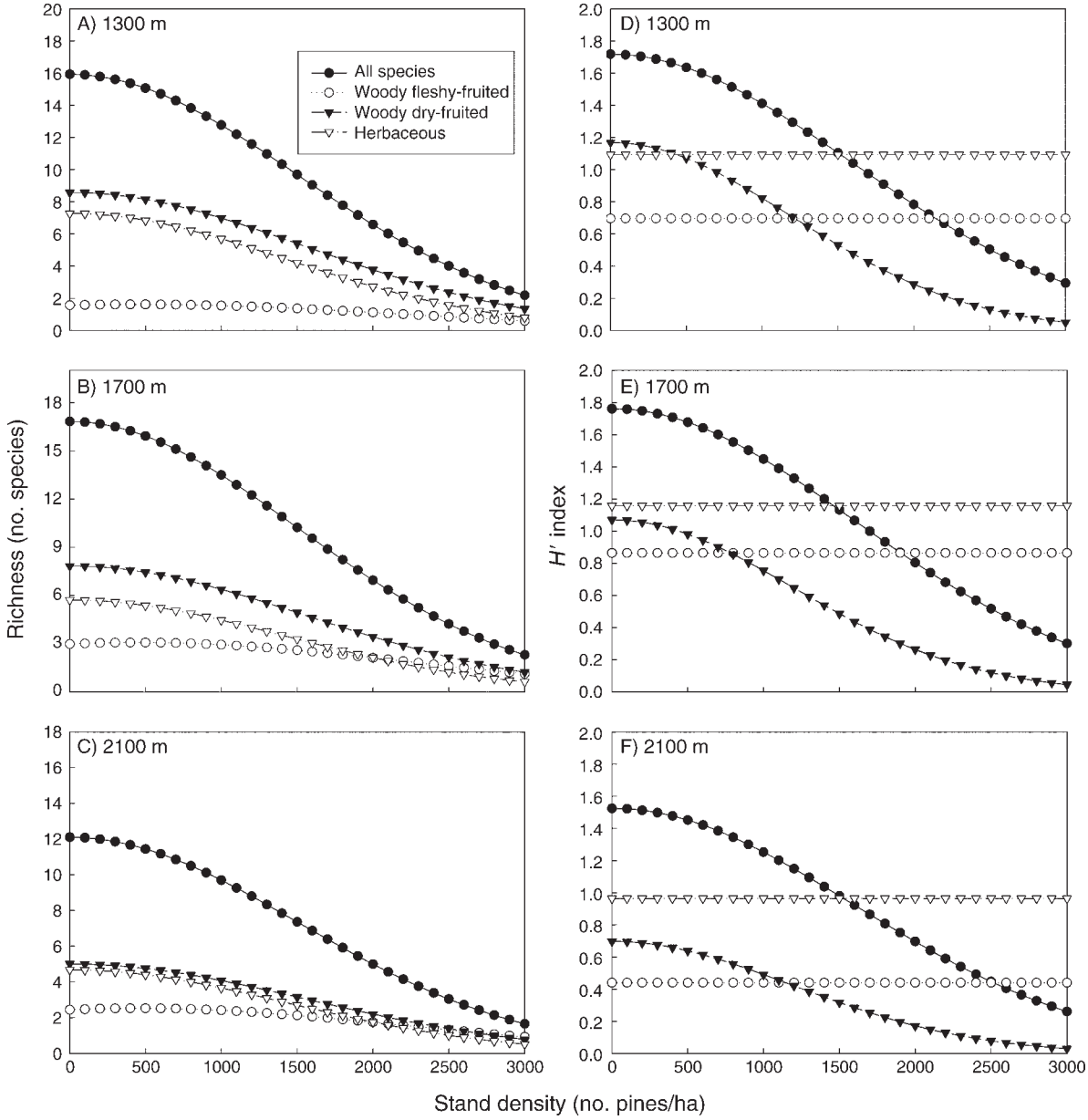

FIG. 6. Effect of stand density on richness (species number) and Shannon's (H') diversity index at different altitudinal levels (low = 1300 m, medium = 1700 m, high = 2100 m). Radiation was fixed at 5 GJ/m^2. Straight lines denote no effect of stand density on H' index values and are included only for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

microclimate, and seedling performance vary along gradients of pine densities.

Our study clearly indicates a prominent importance of distance to seed sources for the colonization of plantations by *Q. ilex*. Thus, seedling abundance diminished by 50% within the first 250 m from the nearest *Q. ilex* forest, and by 80% within 1 km (Fig. 2D). However, some seedlings were found at distances as far as 4 km from the nearest seed source, likely as a result of long-distance dispersal events. In fact, 4 km coincides with the maximum flight distance reported for jays, one of the main dispersers of *Quercus* sp. in Europe (European Jay, *Garrulus glandarius*) and North America (Blue Jay, *Cyanocitta cristata* L.) (Bossema 1979, Johnson and Adkisson 1985). Yet, the rate of long-distance dispersal events does not seem to be sufficient to maintain a sapling bank of *Q. ilex* in such remote patches, since the probability of sapling recruitment tended to zero within shorter distance (2 km). In heterogeneous Mediterranean landscapes, jays move acorns nonrandomly, avoiding some patches (e.g., shrublands and grasslands) and moving most acorns to pine stands, which in turn are high-quality habitats for emergence and survival of *Q. ilex* seedlings (Gómez

PLATE 1. View of dense pine plantations in the Sierra Nevada Mountains of southern Spain. Photo credit: Rut Aspizua Cantón.

2003, 2004). This effective directed dispersal, together with the abundance of *Q. ilex* forests at the landscape scale (>70% of the 442 plantation plots were at ≤2 km from the nearest *Q. ilex* fragment), may be crucial for the successional dynamics towards oak forests that many pine plantations appear to undergo in Sierra Nevada.

Effects of pine plantations on the diversity of vascular plants

Pine plantations had on average lower total plant richness and H' index values than native stands, especially when compared with deciduous broadleaf forests. However, in a detailed analysis, this negative effect appeared only for herbaceous species, and not for woody species. The negative effect on herbaceous species is probably a result of the much higher tree density of plantations in comparison to native fragments, which in turn implies lower understory light levels usually responsible of low herbaceous richness and cover (Harrington and Edwards 1999, Thomas et al. 1999). In any case, pine plantations were not "biological deserts," and several woody and herbaceous species were able to survive within these forest stands. However, plant diversity was very heterogeneous among plantation plots, depending on their local climatic and density characteristics.

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

Stand density had a strong effect on total species richness and evenness, which decreased monotonically along the density gradient (Fig. 6). The impoverished plant diversity of high-density plantations was presumably due to higher seed and establishment limitation than in low-density plantations. On the one hand, bird abundance and richness is in general negatively affected by high canopy densities (especially for jays), thereby reducing the seed flow entering plantations (Vallauri et al. 2002, De la Montaña et al. 2006). A very dense stand structure is also probably a direct obstacle to seed dispersal by wind. On the other hand, thinning experiments have shown species richness to respond positively to tree removal due to competition release and an increased availability of resources (light, water, and nutrients), allowing a greater number of understory species to persist (Thomas et al. 1999, Cummings et al.

2007). It is likely that native species are not adapted to establish in such competitive environments, since natural forests of the area rarely exceed 1000 trees/ha.

When species subgroups were considered, richness of dry-fruited and herbaceous species followed a variation pattern along the density gradient similar to that of total species richness—that is, a monotonically decrease with increasing stand density. On the contrary, richness of fleshy-fruited bird-dispersed species peaked at a moderate tree density (about 500 pines/ha) and was less negatively affected by stand density than in the other subgroups (i.e., richness at maximum stand density reduced only to about 40% of potential, instead of to 20% as in the other subgroups; Fig. 5C). These among-group differences might be influenced by the relationship between dispersal mode and successional status (Huston and Smith 1987). A large number of Mediterranean fleshy-fruited woody species are late-successional shade-tolerant species, whereas pioneer woody species (e.g., Cistaceae, Labiatae, Leguminosae) usually have dry fruits (Herrera 1995). Therefore, fleshy-fruited species will have a comparatively higher probability of persisting in the dark understory of dense plantations than light-demanding dry-fruited woody and herbaceous species. Because shade-tolerance is negatively correlated with drought-tolerance (Niinemets and Valladares 2006), fleshy-fruited species will also benefit more than any other group from the mild microclimate generated by a moderate canopy density.

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 overstory-understory competitive interaction and limits seed inputs from both local (due to a poor understory) 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 change towards oak or pine–oak forests, with the coexistence of these two genera being determined by the stress level (oak dominance being promoted at mesic sites due to greater shade tolerance) and the frequency of disturbance (disturbance promoting pine persistence; Zavala et al. 2000, Zavala and Zea 2004). When at high altitudes, these plantations would be expected to persist as pine forests dominated by *P. sylvestris*, the natural forest formations in the Sierra Nevada tree line.

Management strategies should also take into account that spontaneous colonization of a plantation depends heavily on its distance to natural forest fragments that act as seed sources, as well as on the dispersal ability of the species inhabiting such forests. Thus, among the pool of native tree species available at the landscape scale in Sierra Nevada, *Q. ilex* was the only broadleaf species abundantly found in plantation understories. Other species such as *Q. pyrenaica*, *A. opalus* subsp. *granatense*, or *S. aria* were basically absent, probably due to seed limitation derived from their low regional abundance (most plantations being too far from seed sources of these species) and/or less effective dispersal systems (i.e., wind dispersal in *Acer*). In fact, previous studies indicate that, when seeds are available, all these tree species have high probability of seedling and sapling establishment under moderate shade (as that found in many pine plantations; Gómez-Aparicio et al. 2005, Puerta-Piñero et al. 2007, Mendoza 2008). Enrichment planting will therefore be necessary to increase the diversity and abundance of the seedling bank of pine plantations and recover the mixed natural forests of Sierra Nevada, where *Pinus*, *Quercus*, *Acer*, and *Sorbus* species coexist. Planting will be especially needed in plantations farther than 2 km from the nearest *Q. ilex* forest, where even successful colonization of *Q. ilex* is unlikely. Clearly, seed availability is a major limiting factor in most restoration activities (Young et al. 2001), making seed dispersal a key topic in the theoretical grounds of restoration ecology (Howe and Miriti 2004) and enrichment planting a key activity in restoration practice (e.g., Gardiner et al. 2004, McCament and McCarthy 2005).

Because the ecological characteristics of plantations are strongly heterogeneous at the landscape scale, their use as restoration tools could fail if we do not incorporate the sources of such variability into management planning. We are confident that the results presented in this study will contribute avoiding over-

simplification and promoting the perception of plantations as dynamic systems where successional trajectories and diversity levels are determined by abiotic constraints, complex balances of competitive and facilitative interactions, the spatial configuration of native seed sources, and species life-history traits (dispersal system, shade and drought tolerance).

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Literature Cited

Arévalo, J. R., and J. M. Fernández-Palacios. 2005. From pine plantations to natural stands. Ecological restoration of a *Pinus canariensis* Sweet, ex Spreng forest. Plant Ecology 181: 217–226.

Arrieta, S., and F. Suárez. 2006. Scots pine (*Pinus sylvestris* L.) plantations contribute to the regeneration of holly (*Ilex aquifolium* L.) in Mediterranean central Spain. European Journal of Forest Research 125:271–279.

Barbéro, M., R. Loisel, P. Quézel, D. M. Richardson, and F. Romane. 1998. Pines of the Mediterranean Basin. Pages 153–170 *in* D. M. Richardson, editor. Ecology and biogeography of Pinus. Cambridge University Press, Cambridge, UK.

Barčić, D., V. Hršak, and Ž. Španjol. 2006. The ameliorative effects of pine cultures on forest sites on the island of Rab in Southwest Croatia. Forest Ecology and Management 237: 39–46.

Bell, G. 2000. The distribution and abundance in neutral communities. American Naturalist 155:606–617.

Bellot, J., F. T. Maestre, E. Chirino, N. Hernández, and J. M. Ortiz de Urbina. 2004. Afforestation with *Pinus halepensis* reduces native shrub performance in a Mediterranean semiarid area. Acta Oecologica 25:7–15.

Bossema, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70:1–117.

Brockerhoff, E. G., H. Jactel, J. A. Parrotta, C. P. Quine, and J. Sayer. 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and Conservation 17:925–951.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany 87:1217–1227.

Callaway, R. M. 2007. Positive interactions and interdependence in plant communities. Springer, New York, New York, USA.

Canham, C. D., and M. Uriarte. 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. Ecological Applications 16:62–73.

Cannell, M. G. R. 1999. Environmental impacts of forest monocultures: water use, acidification, wildlife conservation, and carbon storage. New Forests 17:239–262.

Cavelier, J., and A. Tobler. 1998. The effect of abandoned plantations of *Pinus patula* and *Cupressus lusitanica* on soils and regeneration of a tropical montane rain forest in Colombia. Biodiversity and Conservation 7:335–347.

Chazdon, R. L. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458–1460.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. Ecological Monographs 68:213–235.

Cummings, J., and N. Reid. 2008. Stand-level management of plantations to improve biodiversity values. Biodiversity and Conservation 17:1187–1211.

Cummings, J., N. Reid, I. Davies, and C. Grant. 2007. Experimental manipulation of restoration barriers in abandoned eucalypt plantations. Restoration Ecology 15:156–167.

Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, Wisconsin, USA.

De la Montaña, E., J. M. Rey-Benayas, and L. M. Carrascal. 2006. Response of bird communities to silvicultural thinning in Mediterranean maquis. Journal of Applied Ecology 43: 651–659.

Edwards, A. W. F. 1992. Likelihood: expanded edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Espelta, J. M., M. Riba, and J. Retana. 1995. Patterns of seedling recruitment in West-Mediterranean *Quercus ilex* forests influenced by canopy development. Journal of Vegetation Science 6:465–472.

FAO. 2006. Global forest resources assessment 2005: main report. FAO forestry paper 147. Food and Agriculture Organization of the United Nations, Rome, Italy.

Farley, K. A., E. G. Jobbágy, and R. B. Jackson. 2005. Effects of afforestation on water yield: a global synthesis with implications for policy. Global Change Biology 11:1565–1576.

Fortin, M., and J. DeBlois. 2007. Modeling tree recruitment with zero-inflated models: the example of hardwood stands in southern Quebec, Canada. Forest Science 53:529–539.

García-Canseco, V. 2001. Parque Nacional de Sierra Nevada. Canseco Editors, Toledo, Spain.

Gardiner, E. S., J. A. Stanturf, and C. J. Schweitzer. 2004. An afforestation system for restoring bottomland hardwood forests: biomass accumulation of nuttall oak seedlings interplanted beneath Eastern cottonwood. Restoration Ecology 12:525–532.

Gauch, H. G., Jr 1982. Multivariate analysis and community structure. Cambridge University Press, Cambridge, UK.

Goffe, W. L., G. D. Ferrier, and J. Rogers. 1994. Global optimization of statistical functions with simulated annealing. Journal of Econometrics 60:65–99.

Gómez, J. M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26:573–584.

Gómez, J. M. 2004. Importance of burial and microhabitat on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecology 172:287–297.

Gómez-Aparicio, L. 2008. Spatial patterns of recruitment in Mediterranean plant species: linking the fate of seeds, seedlings and saplings in heterogeneous landscapes at different scales. Journal of Ecology 96:1128–1140.

Gómez-Aparicio, L., J. M. Gómez, and R. Zamora. 2005. Microhabitats shift rank in suitability for seedling establishment depending on habitat type and climate. Journal of Ecology 93:1194–1202.

Gómez-Aparicio, L., F. Valladares, and R. Zamora. 2006. Differential light responses of Mediterranean tree saplings: linking ecophysiology with regeneration niche in four co-occurring species. Tree Physiology 26:947–958.

Gómez-Aparicio, L., R. Zamora, J. Castro, and J. A. Hódar. 2008. Facilitation of tree saplings by nurse plants: microhabitat amelioration or protection against herbivores? Journal of Vegetation Science 19:161–172.

Gómez-Aparicio, L., R. Zamora, J. M. Gómez, J. A. Hódar, J. Castro, and E. Baraza. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14:1128–1138.

González-Megías, A., J. M. Gómez, and F. Sánchez-Piñero. 2007. Diversity-habitat heterogeneity relationship at different spatial and temporal scales. Ecography 30:31–41.

Grace, J. B., and D. Tilman. 2003. Perspectives in plant competition. The Blackburn Press, Caldwell, New Jersey, USA.

Greene, D. F., C. D. Canham, K. D. Coates, and P. T. LePage. 2004. An evaluation of alternative dispersal functions for trees. Journal of Ecology 92:758–766.

Haberl, H., K. H. Erb, F. Krausmann, V. Gaube, A. Bondeau, C. Plutzar, S. Gingrich, W. Lucht, and M. Fischer-Kowalski. 2007. Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. Proceedings of the National Academy of Sciences (USA) 104: 12942–12945.

Harrington, T. B., and H. B. Edwards. 1999. Understory vegetation, resource availability, and litterfall responses to pine thinning and woody vegetation control in longleaf pine plantations. Canadian Journal of Forest Research 29:1055–1064.

Hartley, M. J. 2002. Rationale and methods for conserving biodiversity in plantation forests. Forest Ecology and Management 155:81–95.

Herrera, C. M. 1995. Plant–vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. Annual Review of Ecology and Systematics 26: 705–727.

Hewitt, N., and M. Kellman. 2002. Tree seed dispersal among forest fragments: II. Dispersal abilities and biogeographical controls. Journal of Biogeography 29:351–363.

Hilborn, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, New Jersey, USA.

Hobbs, R. J., et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7.

Howe, H. F., and M. N. Miriti. 2004. When seed dispersal matters. BioScience 54:651–660.

Huston, M., and T. Smith. 1987. Plant succession: life history and competition. American Naturalist 130:168–198.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19: 101–108.

Johnson, W. C., and C. S. Adkisson. 1985. Dispersal of beech nuts by Blue Jays in fragmented landscapes. American Midland Naturalist 113:319–324.

Kanowski, J., C. P. Catterall, and G. W. Wardell-Johnson. 2005. Consequences of broadscale timber plantations for biodiversity in cleared rainforest landscapes of tropical and subtropical Australia. Forest Ecology and Management 208: 359–372.

Kunstler, G., W. Thuiller, T. Curt, M. Bouchaud, R. Jouvie, F. Deruette, and J. Lepart. 2007. *Fagus sylvatica* L. recruitment across a fragmented Mediterranean landscape, importance of long distance effective dispersal, abiotic conditions and biotic interactions. Diversity and Distributions 13:799–807.

Lamb, D., P. D. Erskine, and J. A. Parrotta. 2005. Restoration of degraded tropical forest landscapes. Science 310:1628–1632.

Lambert, D. 1992. Zero-inflated Poisson regression, with an application to defects in manufacturing. Technometrics 34:1–14.

LePage, P. T., C. D. Canham, K. D. Coates, and P. Bartemucci. 2000. Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. Canadian Journal of Forest Research 30:415–427.

Liancourt, P., R. M. Callaway, and R. Michalet. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. Ecology 86:1611–1618.

Lookingbill, T., and M. A. Zavala. 2000. Spatial pattern of *Quercus ilex* and *Quercus pubescens* recrutiment in *Pinus halepensis* dominated woodlands. Journal of Vegetation Science 11:607–612.

Lugo, A. E. 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. Forest Ecology and Management 99:9–19.

Ma, M. 2005. Species richness vs. evenness: independent relationship and different responses to edaphic factors. Oikos 111:192–198.

Maestre, F. T., and J. Cortina. 2004. Are *Pinus halepensis* plantations useful as a restoration tool in semiarid Mediterranean areas? Forest Ecology and Management 198:303–317.

Maestre, F. T., J. Cortina, S. Bautista, and J. Bellot. 2003. Does *Pinus halepensis* facilitate the establishment of shrubs under semi-arid climate? Forest Ecology and Management 176:147–160.

McCament, C. L., and B. C. McCarthy. 2005. Two-year response of American chestnut (*Castanea dentata*) seedlings to shelterwood harvesting and fire in a mixed-oak forest ecosystem. Canadian Journal of Forest Research 35:740–749.

Mendoza, I. 2008. Regeneración de la biodiversidad de especies leñosas en un marco de degradación de hábitats mediterráneos de montaña: combinación de interacciones ecológicas y manejo humano. Dissertation. University of Granada, Granada, Spain.

Michalet, R., R. W. Brooker, L. A. Cavieres, Z. Kikvidze, C. J. Lortie, F. I. Pugnaire, A. Valiente-Banuet, and R. M. Callaway. 2006. Do biotic interactions shape the both sides of the humped-back model of species richness in plant communities? Ecology Letters 9:767–773.

Moore, S. E., and H. L. Allen. 1999. Plantation forestry. Pages 400–433 *in* M. L. Hunter, Jr., editor. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, UK.

Niinemets, U., and F. Valladares. 2006. Tolerance to shade, drought and waterlogging of temperate, Northern hemisphere trees and shrubs. Ecological Monographs 76:521–547.

Nogués-Bravo, D., M. B. Araújo, T. Romdal, and C. Rahbek. 2008. Scale effects and human impact on the elevational species richness gradients. Nature 453:216–220.

Paquette, A., A. Bouchard, and A. Cogliastro. 2006. Survival and growth of under-planted trees: a meta-analysis across four biomes. Ecological Applications 16:1575–1589.

Pausas, J. G., C. Bladé, A. Valdecantos, J. P. Seva, D. Fuentes, J. A. Alloza, A. Vilagrosa, S. Bautista, J. Cortina, and R. Vallejo. 2004. Pines and oaks in the restoration of Mediterranean landscapes of Spain: new perspectives for an old practice: a review. Plant Ecology 171:209–220.

Pearson, R. G., and T. P. Dawson. 2005. Long-distance plant dispersal and habitat fragmentation: indentifying conservation targets for spatial landscape planning under climate change. Biological Conservation 123:389–401.

Pérez-Raya, F., J. M. López-Nieto, A. El Aallali, and J. A. Hita-Fernández. 2001. Cartografía y evaluación de la

vegetación del Parque Natural de Sierra Nevada. Consejería de Medio Ambiente, Junta de Andalucía, Spain.

Puerta-Piñero, C., J. M. Gómez, and F. Valladares. 2007. Irradiance and oak seedling survival and growth in a heterogeneous environment. Forest Ecology and Management 242:462–469.

R Development Core Team. 2006. R: a language and environment for statistical computing, version 2.5.0. R Foundation for Statistical Computing, Vienna, Austria.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8:224–239.

Rathbun, S. L., and S. L. Fei. 2006. A spatial zero-inflated Poisson model for oak regeneration. Environmental and Ecological Statistics 13:409–426.

Retana, J., J. M. Espelta, M. Gracia, and M. Riba. 1999. Seedling recruitment. Pages 89–103 *in* F. Rodá, J. Retana, C. A. Gracia, and J. Bellot, editors. Ecology of Mediterranean evergreen oak forests. Springer-Verlag, Berlin, Germany.

Ribbens, E., J. A. Silander, and S. W. Pacala. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. Ecology 75:1794–1806.

Salomonson, V. V., and I. Appel. 2004. Estimating fractional snowcover from MODIS using the normalized difference snow index. Remote Sensing of Environment 89:351–360.

Sánchez, O., F. Sánchez, and M. P. Carretero. 1999. Modelos y cartografía de estimaciones climáticas termopluviométricas para la España peninsular. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain.

Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. BioScience 52:891–904.

Stephens, S. S., and M. R. Wagner. 2007. Forest plantations and biodiversity: a fresh perspective. Journal of Forestry 105: 307–313.

Thomas, S. C., C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. Ecological Applications 9:864–879.

Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Geographical Review 38:55–94.

Vallauri, D. R., J. Aronson, and M. Barbero. 2002. An analysis of forest restoration 120 years after reforestation on badlands in the Southwestern Alps. Restoration Ecology 10:16–26.

Vallejo, R., J. Aronson, J. G. Pausas, and J. Cortina. 2006. Restoration of Mediterranean woodlands. Pages 193–107 *in* J. van Andel and J. Aronson, editors. Restoration ecology. Blackwell Publishing, Oxford, UK.

van Wesenbeeck, B. K., T. van Mourik, J. F. Duivenvoorden, and A. M. Cleef. 2003. Strong effects of a plantation with *Pinus patula* on Andean subparamo vegetation: a case study from Colombia. Biological Conservation 114:207–218.

Weiher, E., and P. A. Keddy. 1999. Relative abundance and evenness patterns along diversity and biomass gradients. Oikos 87:355–361.

White, E., N. Tucker, N. Meyers, and J. Wilson. 2004. Seed dispersal to revegetated isolated rainforest patches in North Queensland. Forest Ecology and Management 192:409–426.

Whittaker, R. H. 1975. Communities and ecosystems. Second edition. MacMillan, New York, New York, USA.

Young, T. P., J. M. Chase, and R. T. Huddleston. 2001. Community succession and assembly: comparing, contrasting, and combining paradigms in the context of ecological restoration. Ecological Restoration 19:5–18.

Zavala, M. A., J. M. Espelta, and J. Retana. 2000. Constraints and trade-offs in Mediterranean plant communities: the case of holm oak–Aleppo pine forests. Botanical Review 66:119–149.

Zavala, M. A., L. Galindo-Jaimes, and M. González-Espinosa. 2007. Models of regional and local stand composition and dynamics of pine-oak forests in the central highlands of Chiapas (Mexico): theoretical and management implications. Pages 223–243 *in* A. C. Newton, editor. Biodiversity loss and conservation of fragmented forest landscapes: the forests of montane Mexico and temperate South America. CAB International, Oxford, UK.

Zavala, M. A., and E. G. Zea. 2004. Mechanisms maintaining biodiversity in Mediterranean pine-oak forests: insights from a spatial simulation model. Plant Ecology 171:197–207.

APPENDIX A

Summary of the 325 vascular plant species found in the forest inventory plots (*Ecological Archives* A019-089-A1).

APPENDIX B

Parameter estimates and support intervals for mean models of natural regeneration and diversity in plantation and natural forest plots (*Ecological Archives* A019-089-A2).

APPENDIX C

Parameter estimates and two-unit support intervals for the most parsimonious regeneration models for each of the five most abundant tree species in plantation understories (*Ecological Archives* A019-089-A3).

APPENDIX D

Parameter estimates and two-unit support intervals for the most parsimonious diversity models (*Ecological Archives* A019-089-A4).