

Large-scale assessment of regeneration and diversity in Mediterranean planted pine forests along ecological gradients

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ABSTRACT

Aim There is increasing concern regarding sustainable management and restoration of planted forests, particularly in the Mediterranean Basin where pine species have been widely used. The aim of this study was to analyse the environmental and structural characteristics of Mediterranean planted pine forests in relation to natural pine forests. Specifically, we assessed recruitment and woody species richness along climatic, structural and perturbation gradients to aid in developing restoration guidelines.

Location Continental Spain.

Methods We conducted a multivariate comparison of ecological characteristics in planted and natural stands of main Iberian native pine species (*Pinus halepensis*, *Pinus pinea*, *Pinus pinaster*, *Pinus nigra* and *Pinus sylvestris*). We fitted species-specific statistical models of recruitment and woody species richness and analysed the response of natural and planted stands along ecological gradients.

Results Planted pine forests occurred on average on poorer soils and experienced higher anthropic disturbance rates (fire frequency and anthropic mortality) than natural pine forests. Planted pine forests had lower regeneration and diversity levels than natural pine forests, and these differences were more pronounced in mountain pine stands. The largest differences in recruitment – chiefly oak seedling abundance – and species richness between planted and natural stands occurred at low-medium values of annual precipitation, stand tree density, distance to *Quercus* forests and fire frequency, whereas differences usually disappeared in the upper part of the gradients.

Main conclusions Structural characteristics and patterns of recruitment and species richness differ in pine planted forests compared to natural pine ecosystems in the Mediterranean, especially for mountain pines. However, management options exist that would reduce differences between these forest types, where restoration towards more natural conditions is feasible. To increase recruitment and diversity, vertical and horizontal heterogeneity could be promoted by thinning in high-density and homogeneous stands, while enrichment planting would be desirable in mesic and medium-density planted forests.

Keywords

Continental Spain, management, naturalization, plantation, recruitment limitation, woody species richness.

INTRODUCTION

Forests cover more than 30% of the terrestrial biosphere (FAO, 2010) and harbour around two-thirds of terrestrial biological diversity (MEA, 2005). These reservoirs of biodiversity are

threatened by ongoing deforestation and forest degradation processes (FAO, 2010), and increasingly also by new pressures such as climatic change (Dale *et al.*, 2001). Restoration is a promising approach to counteract loss of forests and related ecosystem services (Lamb *et al.*, 2005; Chazdon, 2008).

Restoration activities focus on contrasting but complementary strategies, namely 'passive restoration' or forest regrowth based on secondary succession and 'active restoration' or tree plantations (Mansourian, 2005). World-wide afforestations have reforested more land than forest regrowth during the period 2000–10 (4.9 vs. 2.9 million ha yr⁻¹, respectively, FAO 2010). Tree planting on deforested land is a rapid recovery strategy that may increase both diversity and provisioning of ecosystem services (Rey Benayas *et al.*, 2009).

In general, planted forests have chiefly been used in the past for timber and fibre production, but also serve protective (e.g. soil erosion mitigation or basin conservation) and/or recreational purposes (FAO, 2006; Evans, 2009). Currently, there is an increasing demand for multipurpose tree plantations (Paquette & Messier, 2010) because of policies addressing wood supply (Sutton, 1999), restoration of abandoned farmland (Rey Benayas, 2005) and carbon sequestration (Jackson *et al.*, 2005; Canadell & Raupach, 2008), which has led to an increase in the planted forest surface (FAO, 2010). World-wide planted forests, however, are highly controversial, and plantations are often considered as 'green deserts' (Stephens & Wagner, 2007; Bremer & Farley, 2010; Felton *et al.*, 2010) or 'novel ecosystems' (e.g. Hobbs *et al.*, 2006) that do not completely achieve the ecosystem services provided by natural forests (Rey Benayas *et al.*, 2009). Furthermore, some authors have highlighted trade-offs between ecosystem services provided by tree plantations (e.g. carbon sequestration versus soil water availability, Jackson *et al.*, 2005). Thus, there is an urgent need for planted forests to act as sustainable systems that meet standards similar to those of natural forests in terms of biodiversity conservation and ecosystem functioning (Evans, 2009; Bremer & Farley, 2010). Although a number of studies have compared the structure and function of plantations and paired natural forests (e.g. Lugo, 1992; Gómez-Aparicio *et al.*, 2009), a few have examined both forest types across extensive regions.

The Mediterranean Basin is one of the world regions with the largest proportion of planted forests (FAO, 2010). Large-scale afforestation programs were initiated in the late 19th century to restore degraded lands after thousands of years of human exploitation (Barbero *et al.*, 1998). The Spanish Reforestation Plan of 1939 is a good example of such large-scale reforestations, because it involved around 3.5 million ha of planted forests from 1940 to 1995 (Montero, 1997). Pines were the most commonly used tree species because of their fast growing pioneer performance, providing rapid ground coverage and eventually facilitating establishment of late successional hardwoods (Zavala & Zea, 2004). However, the achievements of these afforestation policies have often been questioned. For example, the lack of post-plantation operations – because of elevated costs and low timber production (Madrigal, 1998) – has often resulted in high-density stands with arrested succession (i.e. lack of pine replacement by later successional species such as hardwoods, Chirino *et al.*, 2006). Secondary succession may also be impeded in planted pine forests because of low seed supply (García *et al.*, 2010) as avian diversity and seed disperser preferences are negatively influ-

enced by a simplified forest structure (López & Moro, 1997) and its surrounding vegetation (Zamora *et al.*, 2010). As a result, planted forests may exhibit poorer regeneration and lower species richness than adjacent natural forests (Gómez-Aparicio *et al.*, 2009).

After more than 60 years of the massive Spanish afforestation effort, the characteristics of these planted pine forests and their consequences for key functional and structural attributes of the forest community, such as recruitment and species diversity, remain largely unexplored. We addressed the following objectives: (1) to identify differences between planted and natural pine forests, particularly those regarding edapho-climatic conditions, structural features and disturbance regimes; (2) to assess patterns of pine and oak recruitment and woody species richness in both ecosystems – planted and natural – along climatic, vegetation structure and disturbance gradients; and (3) to propose specific management and restoration recommendations intended to reduce differences between planted forests and natural pine forests. These objectives, based on a comparison of planted forests versus reference natural systems (Dudley, 2005), will enable us to generate valuable theoretical and practical information on diversity and succession in Mediterranean pine plantations.

METHODS

Study area and data set

The Iberian Peninsula presents a wide altitudinal range (sea level–3500 m) and a steep climatic gradient – from arid Mediterranean to cool temperate climates – all of which confers this region with high habitat and species diversity. Pine forests constitute a structural component of Mediterranean plant communities and spatially, they may coexist with, alternate with or be segregated from hardwoods (Blanco *et al.*, 1997). Pine forests can be the successional end point under severe environmental conditions, such as dry or cold climates or shallow and rocky soils (Barbero *et al.*, 1998; Zavala *et al.*, 2000).

We built a spatial database by combining three types of data sources: the Spanish Forest Inventory (SFI hereafter), the Spanish Regions of Provenance for Forest Species (SRP hereafter) and several cartographic sources at national scale. We used permanent stands that had been surveyed for the second (1986–96, 2SFI hereafter) and the third SFI (1997–2007, 3SFI hereafter) and that were distributed over forest ecosystems on a 1-km² cell grid (Villaescusa & Díaz, 1998). Each SFI stand included four concentric circular sub-plots of 5, 10, 15 and 25 m radius. In these sub-plots, an adult tree was sampled if its diameter at breast height (d.b.h.) was 7.5–12.4, 12.5–22.4, 22.5–42.5 and ≥ 42.5 cm, respectively. Height, d.b.h. and species name were recorded for each adult tree included in the stand.

The SRP was ascertained for each species according to historical information regarding planted versus natural origin (Ceballos, 1966), which was later refined by genetic analyses

and other regional information (Alía *et al.*, 2009). Our definition of ‘natural pine forests’ was based on SRP autochthonous forests, that is, a forest originated by natural regeneration from local or nearby native sources (Alía *et al.*, 2005). ‘Natural pine forests’ in this study excluded all forests planted during the 20th century and included all forests established through natural regeneration (FAO, 2006).

The spatial vector database of the SRP for pine species and the UTM coordinates of the SFI stands were combined using ARCGIS 9.2 (ESRI Inc., Redlands, CA, USA). Where the same adult tree species was observed in the SRP and the SFI, the stand was included in this study. A total of 32,719 stands were selected with the presence of the adult species *Pinus halepensis* Mill., *Pinus pinea* L., *Pinus pinaster* Ait., *Pinus nigra* Arnold., and *Pinus sylvestris* L. (Fig. 1). We did not consider *P. uncinata* Mill., because 99% of the stands were natural, nor *P. radiata* D. Don, because all stands were planted. About 65.8% of the pine stands were monospecific and the remaining 34.2% were mixed stands.

Analysed variables

Each of the 32,719 stands was characterized by 26 abiotic, six biotic and four anthropic variables. The abiotic variables included four topographic, 19 climatic and three edaphic variables. The *topographic* variables included altitude (m), slope (degrees), aspect (degrees) and insolation (hours per year) and were calculated from a SRTM V1 digital elevation model with a 1-km² spatial resolution (Shuttle Radar Topographic Mission, <http://www2.jpl.nasa.gov/srtm/>). The *climatic variables*, calculated from Gonzalo’s (2008) map with a 1-km² spatial resolution, were annual precipitation (mm), seasonal precipitation (i.e. in spring, summer, fall and winter), mean annual temperature (°C), seasonal temperature (°C), mean temperature of the warmest month (°C), mean minimum temperature of the month with lowest mean annual temperature (°C), annual potential evapotranspiration (Thornthwaite, 1948), annual water surplus (mm, sum of the positive differences between annual precipitation and potential

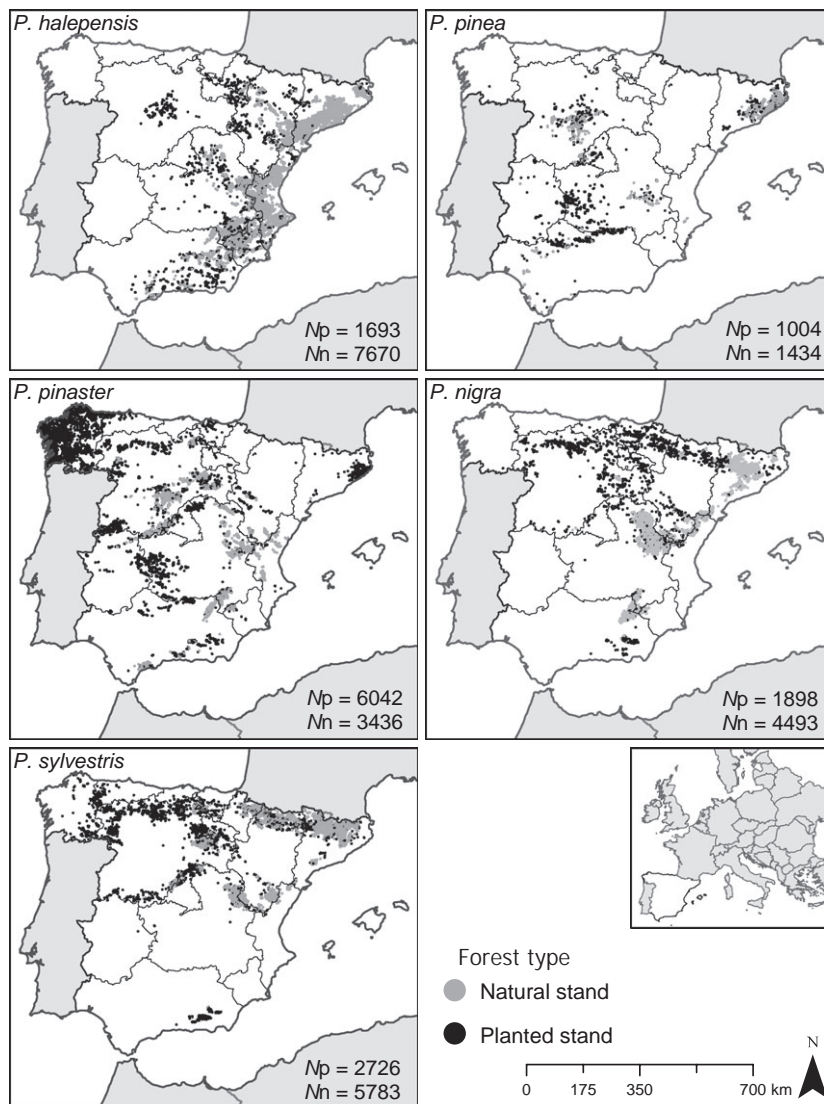


Figure 1 Occurrence of planted (Np) and natural (Nn) pine stands of *Pinus halepensis*, *Pinus pinea*, *Pinus pinaster*, *Pinus nigra* and *Pinus sylvestris* included in the study, from the Spanish Forest Inventory. Map projection UTM 30N, European Datum 1950.

evapotranspiration), annual water deficit (mm, sum of the negative differences between annual precipitation and potential evapotranspiration), drought length (number of months in which potential evapotranspiration exceeded precipitation) and aridity index (ratio between annual potential evapotranspiration and mean annual precipitation, UNEP, 1997). The relationship between the topographic and climatic variables was explored using Principal Component Analysis in R (R Development Core Team, 2009). The first axis of the PCA (explaining 53.5% of the variance) was strongly correlated with annual precipitation and the second axis (explaining 21.8%) with mean annual temperature. Therefore, these two variables were selected for our modelling analysis as being representative of the climatic conditions for each pine stand. The three edaphic variables obtained from 3SFI were rockiness (0–25%, 25–50%, > 50%), soil texture (sandy, loam and clay) and soil pH (acid (pH ≤ 6), neutral (pH = 7) or basic (pH ≥ 8)).

The *biotic variables* calculated from 3SFI were stand basal area (m² ha⁻¹), stand tree density (No. trees per ha), coefficient of variation of tree diameter (ratio of the standard deviation to the mean of the diameters of all trees in the stand), monospecific character of the stand (ratio of a particular pine species' basal area to total stand basal area), distance to the nearest *Quercus* forest and natural mortality (basal area in m² ha⁻¹ of the trees that were present in the 3SFI and had died between the 2SFI and the 3SFI). Distance to the nearest *Quercus* forest was calculated with ARCGIS 9.2 (ESRI Inc.) as the minimum distance between pine stands of the 3SFI and polygons of the Spanish Forest Map with *Quercus* presence at scale 1:50,000 (MARM, <http://www.marm.es/>).

The *anthropic variables* were anthropic mortality, distance to the nearest road, fire frequency and conservation status. Anthropic mortality was calculated as the basal area (m² ha⁻¹) of the trees that had been removed in the period between the 2SFI and the 3SFI. Distance to the nearest road was calculated from data available at the Spanish Spatial Data Infrastructure portal (IDEE, <http://www.idee.es/>). Fire frequency was calculated for the same survey period between the 2SFI and 3SFI (1986–2007) at municipality level (MARM, <http://www.marm.es/>). The conservation status was calculated by overlapping the 3SFI stand coordinates with the network of nationally designated natural protected areas (presence/absence) using ARCGIS 9.2.

The response variables were pine and oak recruitment (number of pine and oak seedlings per stand, respectively) and woody species richness. In the 5-m radius circle of the 3SFI (area 78.5 m²), abundance of seedlings (d.b.h. < 2.5 cm or height < 1.3 m) was quantified using a semi-quantitative scale (low: 1–4 seedlings per ha, medium: 5–15 seedlings per ha or high: > 15 seedlings per ha). To transform these data into a continuous scale that could be used in regression analyses, we selected the lowest value of each range as a conservative approach. Woody species richness was calculated as the number of trees and shrub species included in the 25-m radius circular plot of the 3SFI.

Statistical analyses

Environmental and structural characteristics of pine forests

We performed three separate analyses to compare the characteristics of planted pine forests and natural pine forests along environmental gradients. Firstly, we used semi-parametric multivariate analyses of variance (PERMANOVA 10,000 permutations; adonis library *vegan* in R, Oksanen *et al.*, 2010) to examine differences between the two forest types as regards the five abiotic (two climatic and three edaphic), six biotic and four anthropic variables. Secondly, we conducted a Canonical Correspondence Analysis (CCA library *vegan* in R, Oksanen *et al.*, 2010) to relate pine abundance (estimated as basal area) to the same abiotic, biotic and anthropic variables as those used in the PERMANOVA. Thirdly, the differences for each environmental variable in planted and natural forest stands were identified by means of the Wilcoxon test.

Seedling recruitment patterns

We examined differences in mean pine and oak seedling abundance between planted and natural forest stands using Wilcoxon tests. Then, we fitted regression models using Generalized Linear Models (GLM) with a negative binomial error distribution and a log link function. A negative binomial distribution was preferred over a Poisson distribution because the response variables showed over-dispersion (Bolker, 2008). The predictor variables included in the models were: forest type (planted versus natural), climatic variables, edaphic factors, biotic variables (distance to the nearest *Quercus* forest was considered only for *Quercus* recruitment) and anthropic variables. Continuous variables were included as a linear and second-order polynomial term to select the best transformation of the explanatory variables to account for nonlinearity (Kunstler *et al.*, 2007). First, a step-wise procedure using the Akaike Information Criterion was applied to select the main variables affecting recruitment (stepAIC library *MASS* in R, Venables & Ripley, 2002). Then, the interactions between forest type and the variables selected in the previous step were tested to explore whether the effect of a given variable differed between planted and natural forests. The response curves for the explanatory variables were computed between the minimum and maximum values measured in planted and natural stands, with the values of other continuous variables fixed at the mean observed (Table 1), and the most common value for categorical variables.

Woody species richness patterns

We used the same modelling approach as for seedling recruitment to examine patterns of woody species richness. Firstly, the Wilcoxon test was applied to examine woody species richness differences between planted and natural forests. Secondly, GLM models were run using a Poisson distribution and the log link function to explore variations in species richness along environmental gradients.

Table 1 Mean values and standard error of the abiotic, biotic and anthropic variables of planted and natural forest stands of the five pine species studied.

	<i>Pinus halepensis</i>		<i>Pinus pinea</i>		<i>Pinus pinaster</i>		<i>Pinus nigra</i>		<i>Pinus sylvestris</i>	
	Planted	Natural	Planted	Natural	Planted	Natural	Planted	Natural	Planted	Natural
Mean annual temperature (°C)	13.8 ± 0.04	14 ± 0.01	14.5 ± 0.05	13.6 ± 0.05	12.8 ± 0.02	11.8 ± 0.03	10.7 ± 0.03	11.1 ± 0.02	9.5 ± 0.03	9.4 ± 0.02
Annual precipitation (mm)	520 ± 3.74	541 ± 1.62	632 ± 4.17	623 ± 4.11	1110 ± 5.57	693 ± 3.95	773 ± 5.78	756 ± 2.41	964 ± 5	963 ± 2.75
Soil rockiness		*		*		*		*		*
Soil texture		*		*		*		*		*
Soil pH		*		*		*		*		*
Stand basal area (m ² ha ⁻¹)	10.3 ± 0.2	10.6 ± 0.09	12.5 ± 0.27	14.4 ± 0.23	19 ± 0.17	17.7 ± 0.21	17.8 ± 0.27	14.9 ± 0.15	21.4 ± 0.26	21.7 ± 0.17
Stand density (trees per ha)	472 ± 10.18	449.4 ± 4.33	415.1 ± 12.62	412.7 ± 10.63	577.6 ± 6.13	418.8 ± 6.79	842.7 ± 13.04	601.3 ± 7.92	848.2 ± 11.38	712.2 ± 6.91
Distance to <i>Quercus</i> forest (m)	9457 ± 309.26	6681 ± 103.16	2131 ± 124.16	2929 ± 112.71	6626 ± 107.34	3937 ± 104.16	6300 ± 232.36	2327 ± 56.22	6648 ± 154.84	6262 ± 107.7
Coefficient of variation of tree diameter	0.27 ± 0.003	0.306 ± 0.002	0.27 ± 0.004	0.332 ± 0.004	0.314 ± 0.002	0.305 ± 0.002	0.258 ± 0.003	0.347 ± 0.002	0.257 ± 0.002	0.337 ± 0.002
Monospecific character	0.96 ± 0.00	0.93 ± 0.00	0.89 ± 0.01	0.8 ± 0.01	0.8 ± 0.00	0.94 ± 0.00	0.9 ± 0.00	0.86 ± 0.00	0.91 ± 0.00	0.83 ± 0.00
Natural mortality (m ² ha ⁻¹)	0.2 ± 0.02	0.2 ± 0.01	0.3 ± 0.03	0.3 ± 0.03	0.3 ± 0.02	0.4 ± 0.02	0.1 ± 0.01	0.3 ± 0.02	0.3 ± 0.02	0.5 ± 0.02
Anthropic mortality (m ² ha ⁻¹)	0.5 ± 0.05	0.5 ± 0.02	1.1 ± 0.1	1.3 ± 0.08	2.9 ± 0.08	1.8 ± 0.07	0.9 ± 0.07	0.8 ± 0.04	1.3 ± 0.08	1.1 ± 0.04
Fire frequency	53.1 ± 1.6	50.1 ± 0.59	68 ± 1.94	52.1 ± 1.77	379.3 ± 6.34	64.3 ± 2.04	37.1 ± 1.43	49.4 ± 1.12	128 ± 5.69	27.1 ± 0.66
Distance to road	5859 ± 116.93	5785 ± 49.23	8131 ± 213.93	3910 ± 86.12	6319 ± 80.54	7023 ± 96.55	6151 ± 106.4	8654 ± 101.43	6830 ± 93.24	7668 ± 87.79

Differences were considered significant at $P < 0.00357$ after Bonferroni corrections for 14 variables and are marked in bold or with asterisks (*) in factor variables.

RESULTS

Environmental and structural characteristics of pine forests

The characteristics of planted and natural pine forest stands were significantly different for all pine species (PERMANOVA, $F_{P. halepensis} = 55.6$, $F_{P. pinea} = 109.7$, $F_{P. pinaster} = 306.8$, $F_{P. nigra} = 160.2$, $F_{P. sylvestris} = 27.5$, $P < 0.001$ in all cases).

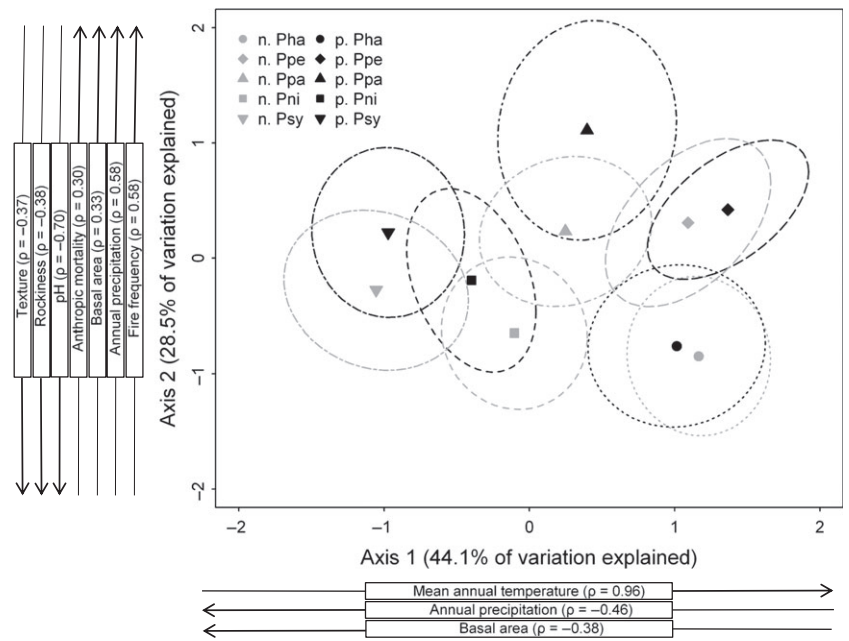
The first two CCA axes explained 72.6% of the variation observed in the data, and clearly separated planted from natural stands of the five pine species, especially for *P. pinaster*, *P. nigra* and *P. sylvestris* (Fig. 2). The first axis was positively correlated with mean annual temperature and negatively correlated with annual precipitation and stand basal area. These results showed an aridity gradient along axis 1, where the main differences between planted and natural stands varied strongly depending on the pine species (Fig. 2). *P. pinaster* and *P. pinea* had higher mean temperature in planted stands than in natural stands, whereas *P. halepensis* and *P. nigra* showed the opposite pattern (Table 1). The second axis of the CCA showed a negative correlation with soil texture, rockiness and pH, and a positive correlation with fire frequency, annual precipitation, stand basal area and anthropic mortality (Fig. 2). These results suggested a gradient along axis 2 where planted forest stands were characterized by higher intensity of disturbance (fire frequency and anthropic mortality) and poorer soils (acid and rocky) than natural forest stands.

Structural characteristics of planted pine forests were in general significantly different from natural pine forests (Table 1). Pine plantations exhibited a higher density and monospecific character, shorter distances to oak forests and a lower coefficient of variation of tree diameter than natural forests.

Seedling recruitment patterns

Both pine and oak seedling abundance was generally lower in planted than in natural forest stands (Table S1, in Supporting Information). Forest type (planted versus natural) was one of the most explicative variables for pine recruitment (except for *P. pinea*), explaining the largest deviance in the two mountain pines. Climatic variables, biotic variables (mainly tree density or basal area) and anthropic variables (mainly fire frequency) generally explained a high proportion of deviance in the pine recruitment GLM models (Table 2). Forest type was also a significant explanatory factor of oak recruitment in most pine forests (all but *P. halepensis* forests), but it usually explained a lower proportion of deviance than climatic factors, tree density, basal area and distance to the nearest *Quercus* forest. Anthropic factors also explained a low proportion of the deviance in oak seedling GLM models compared to abiotic and biotic factors (Table 2). A nonlinear response of pine and oak recruitment was observed along all the environmental gradients explored (polynomial transformation of order 2, Table 2).

Figure 2 Canonical Correspondence Analysis (CCA) of the environmental variables characterizing natural (n.) and planted (p.) forest stands of *Pinus halepensis* (Pha), *Pinus pinea* (Ppe), *Pinus pinaster* (Ppa), *Pinus nigra* (Pni) and *Pinus sylvestris* (Psy). Variables with Spearman correlations > 0.3 are shown on the CCA axes. Confidence ellipses of point scores were included using standard deviation with a confidence interval of 95%.



We detected significant interactions between forest type and several of the abiotic, biotic and anthropic variables for both pine and oak recruitment. The interactions that consistently explained a larger proportion of the deviance across canopy pine species were mainly annual precipitation, tree density, distance to the nearest *Quercus* forest and fire frequency (Table S2). The largest recruitment differences between forest types generally occurred at intermediate values along the annual precipitation gradient, with lower differences at the extremes of this gradient (Fig. 3a). In Mediterranean pine forests (*P. halepensis* and *P. pinaster*), the largest recruitment differences between forest types also occurred at intermediate values along the tree density gradient (*c.* 1000 trees per ha; Fig. 3b). However, oak seedling abundance increased along the tree density gradient in mountain pine stands (Fig. 3b). Distance to the nearest *Quercus* forest had a negative effect on oak seedling abundance in all pine stands except those of *P. sylvestris*. The detrimental effect of this variable on oak recruitment was more pronounced in natural than in planted pine stands (*P. pinaster* and *P. nigra*; Table S2; Fig. 3c). Fire frequency had an overall negative effect on seedling recruitment, particularly for oaks, with largest differences in recruitment between planted and natural forest stands occurring mostly at low fire frequency values (Fig. 3d).

Woody species richness patterns

Planted forest stands had on average lower species richness than natural forest stands (Table S3). Forest type was the second most important factor in terms of explained deviance for three of the GLM pine species models (*P. pinaster*, *P. nigra* and *P. sylvestris*; Table 3). Only climatic factors explained a larger proportion of deviance than forest type in the richness

models. Species richness was also strongly affected by soil factors (pH and texture), monospecific character, coefficient of variation of tree diameter and fire frequency (Table 3).

We detected significant interactions between forest type and several of the abiotic, biotic and anthropic variables analysed. The interactions that consistently explained a larger proportion of the deviance for most pine species were those with climate variables, tree density, coefficient of variation of tree diameter and fire frequency (Table S4). Species richness usually showed a Gaussian response along the precipitation gradient. The largest richness differences between forest types occurred at intermediate values and decreased towards the extremes of the precipitation gradient (Fig. 4a). The effect of tree density on species richness differed significantly between planted and natural stands of *P. pinea* and *P. sylvestris* (Table S4). Maximum species richness in natural forest stands occurred at intermediate values of tree density (around 1000 trees per ha), where the largest differences in species richness between forests type were also found (Fig. 4b). Species richness for even-sized (i.e. with low values for coefficient of variation of tree diameter) planted forest stands was lower than those observed in natural forest stands, but these differences decreased and even disappeared for uneven-sized stands (Fig. 4c). Fire frequency had a strong negative effect on species richness, especially in natural forest stands, and the largest differences between forest types consistently occurred at low fire frequency values (Fig. 4d).

DISCUSSION

Iberian planted pine forests occurred on average on sites which differed in climatic conditions, soils and perturbation regimes with respect to natural pine forests. Planted stands exhibited a

Table 2 Best models of pine and oak recruitment in forest stands of the five pine species studied. The selected transformation (*poly* (2) is polynomial transformation of order 2), degrees of freedom (d.f.), model deviance (M. Dev.), explanatory variable deviance (Dev.) and probabilities of chi-square tests of the variable effects are given.

	<i>Pinus halepensis</i>				<i>Pinus pinea</i>				<i>Pinus pinaster</i>				
	P. seed. (M. Dev.: 0.06)		Q. seed. (M. Dev.: 0.29)		P. seed. (M. Dev.: 0.16)		Q. seed. (M. Dev.: 0.12)		P. seed. (M. Dev.: 0.11)		Q. seed. (M. Dev.: 0.06)		
	d.f.	Dev.	<i>P</i> (χ^2)	d.f.	Dev.	<i>P</i> (χ^2)	d.f.	Dev.	<i>P</i> (χ^2)	d.f.	Dev.	<i>P</i> (χ^2)	
Forest type	1	94.7	< 0.0001										
Temperature <i>poly</i> (2)	2	581.4	< 0.0001	2	157.13	< 0.0001	2	33.14	< 0.0001	1	53.9	< 0.0001	
Precipitation <i>poly</i> (2)	2	1207.9	< 0.0001	2	15.03	< 0.0001	2	100.2	< 0.0001	2	104.1	< 0.0001	
Soil rockiness	2	45	< 0.0001	2	98.1	< 0.0001	2	22.6	< 0.0001	2	47.1	< 0.0001	
Soil texture	2	10.1	0.0063	2	3.7	0.1583		2	32.36	< 0.0001	2	44.1	< 0.0001
Soil pH	2	9.6	0.0071	2	27	< 0.0001	2	2	1.19	0.5508	2	52.1	< 0.0001
Basal area <i>poly</i> (2)	2	52.3	< 0.0001	2	231.1	< 0.0001	2	26.01	< 0.0001	2	54	< 0.0001	
Tree dens. <i>poly</i> (2)	2	10	0.0019	2	8.5	0.0145	2	92.51	< 0.0001	2	43.3	< 0.0001	
CVd <i>poly</i> (2)	2	17.3	0.0003	2	142	< 0.0001	2	7.08	0.0290	2	122	< 0.0001	
Monosp. <i>poly</i> (2)	2	84.8	< 0.0001	2	303.4	< 0.0001	2	24.62	< 0.0001	2	545.7	< 0.0001	
Dist. <i>Quercus poly</i> (2)				2	138	< 0.0001	2	40.22	< 0.0001	2	94.1	< 0.0001	
Nat. mor. <i>poly</i> (2)	2	17.6	< 0.0001	2	12.7	0.0018	2	9.74	0.1091	2	7.5	0.0235	
Ant. mor. <i>poly</i> (2)	2	14.5	< 0.0001	2	6.2	0.0460	2	4.43	< 0.0001	2	104.5	< 0.0001	
Road <i>poly</i> (2)	2	9.9	0.0047	2	31.59	< 0.0001	2	32.17	< 0.0001	2	16.1	0.0003	
Fire <i>poly</i> (2)	2	16.6	< 0.0001	2	77	< 0.0001	2	27.89	< 0.0001	2	18.06	0.0001	
Protection				1	17.6	< 0.0001	1	7.08	0.0078	1	8	0.0047	
	<i>Pinus nigra</i>				<i>Pinus sylvestris</i>								
	P. seed. (M. Dev.: 0.15)		Q. seed. (M. Dev.: 0.11)		P. seed. (M. Dev.: 0.09)		Q. seed. (M. Dev.: 0.19)						
	d.f.	Dev.	<i>P</i> (χ^2)	d.f.	Dev.	<i>P</i> (χ^2)	d.f.	Dev.	<i>P</i> (χ^2)	d.f.	Dev.	<i>P</i> (χ^2)	
Forest type	1	418	< 0.0001	1	125	< 0.0001	1	240.6	< 0.0001	1	70.2	< 0.0001	
Temperature <i>poly</i> (2)	2	34.4	< 0.0001	2	263.1	< 0.0001	2	52.0	< 0.0001	2	1177	< 0.0001	
Precipitation <i>poly</i> (2)	2	54.6	< 0.0001	2	86.2	< 0.0001	2	235.1	< 0.0001	2	145.3	< 0.0001	
Soil rockiness	2	48.5	< 0.0001	2	64	< 0.0001	2	16.8	0.0002	2	23.6	< 0.0001	
Soil texture	2	1.4	0.4889	2	4.8	0.0902		2	15.2	0.0005			
Soil pH	2	21.5	< 0.0001	2	13.4	0.0012		2	8.2	0.0169			
Basal area <i>poly</i> (2)	2	153	< 0.0001	2	44.4	< 0.0001	2	57.7	< 0.0001	2	14.9	0.0006	
Tree dens. <i>poly</i> (2)	2	37.3	< 0.0001	2	61.8	< 0.0001	2	23.2	< 0.0001	2	52.6	< 0.0001	
CVd <i>poly</i> (2)	2	36.1	< 0.0001	2	35.1	< 0.0001	2	66.7	< 0.0001	2	72.5	< 0.0001	
Monosp. <i>poly</i> (2)	2	312	< 0.0001	2	49	< 0.0001	2	72.5	< 0.0001	2	72.5	< 0.0001	
Dist. <i>Quercus poly</i> (2)				2	24.4	< 0.0001							
Nat. mor. <i>poly</i> (2)	2	30.7	< 0.0001	2	15.2	0.0005	2	43.2	< 0.0001	2	6.5	0.0382	
Ant. mor. <i>poly</i> (2)	2	5.8	0.0558	2	5.8	0.0562	2	30.0	< 0.0001				
Road <i>poly</i> (2)	2	9.3	0.0094	2	28.5	< 0.0001	2	84.7	< 0.0001	2	84.7	< 0.0001	
Fire <i>poly</i> (2)	2	14.8	0.0006	2	59.4	< 0.0001	2	43.4	< 0.0001	2	98.2	< 0.0001	
Protection							1	39.4	< 0.0001				

Temperature: mean annual temperature; Precipitation: annual precipitation; Basal area: basal area ($\text{m}^2 \text{ha}^{-1}$); Tree dens.: tree density (trees per ha); CVd: coefficient of variation of tree diameter; Monosp.: monospecific character (%); Dist. *Quercus*: distance to the nearest *Quercus* forest (m); Nat. mor.: basal area lost by natural mortality ($\text{m}^2 \text{ha}^{-1}$); Ant. mor.: basal area lost by anthropic mortality ($\text{m}^2 \text{ha}^{-1}$); Road: distance to road (m); Fire: fire frequency; Protection: protected area. Differences were considered significant at $P(\chi^2) < 0.05$ and are marked in bold.

higher tree density, a greater tendency to form even-sized populations, and a lower recruitment and woody species richness than natural stands. Differences between forest types were species-specific, being more pronounced for mountain than for Mediterranean pine species, and varied strongly along

the ecological gradients selected. These patterns suggest the need to develop species- and site-specific actions that would enable the reorientation of planted forests towards states that are structurally and functionally more similar to those of natural forests.

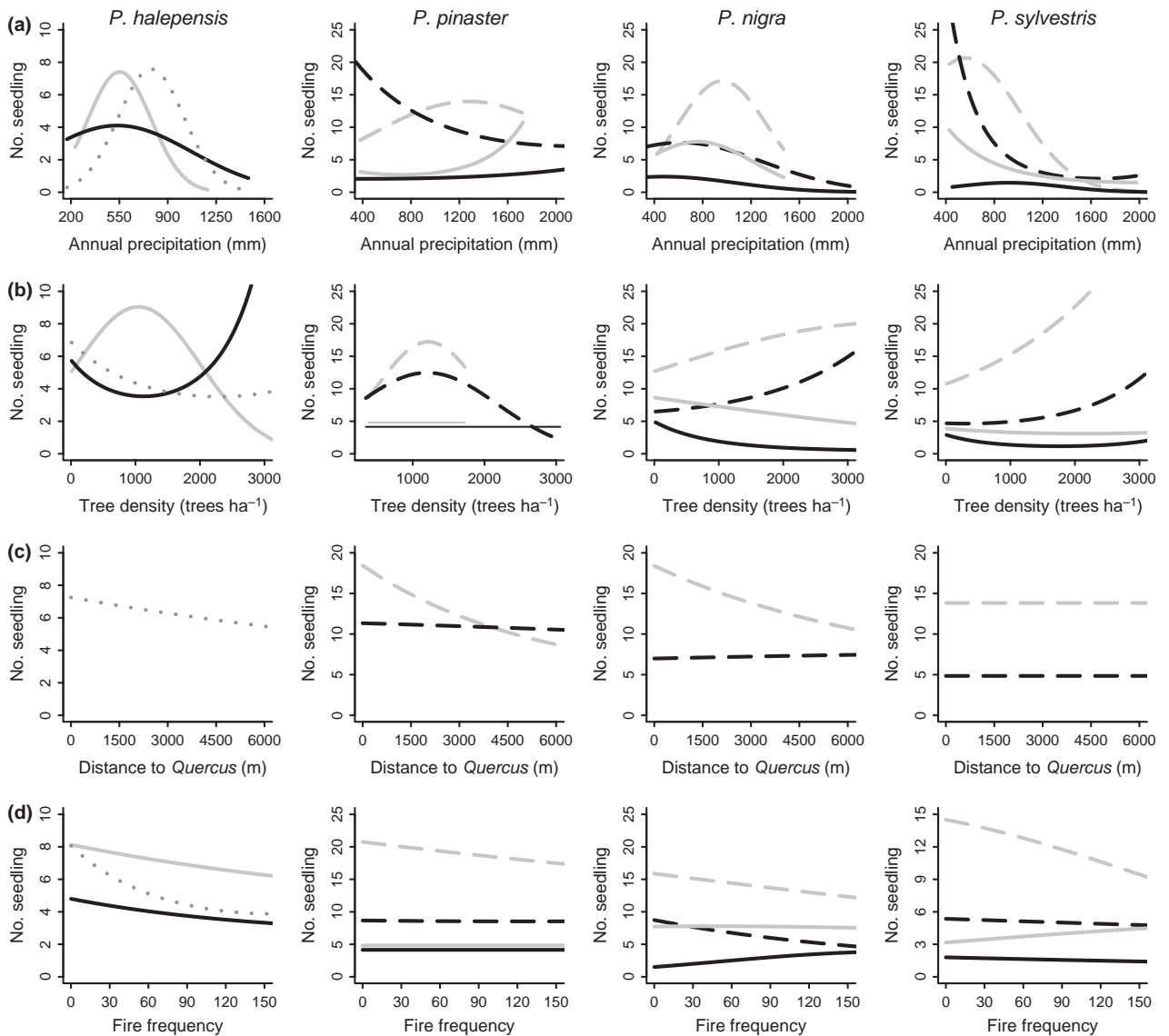


Figure 3 Form of the relationships between predicted pine recruitment (continuous line) and oak recruitment (dashed line) along annual precipitation (a); tree density (b); distance to the nearest *Quercus* forest (c); and fire frequency (d) in planted (black line) and natural (grey line) forest stands of *Pinus halepensis*, *Pinus pinaster*, *Pinus nigra* and *Pinus sylvestris*. *Pinus pinea* was not included in this analysis because forest type had a non-significant effect on pine and oak seedling abundance. Interactions significant between forest type and environmental variables are available in Table S2, and straight lines denote a non-significant effect of the variable on recruitment and are shown in these figures only for comparative purposes. As forest type was not selected by the best generalized linear models of *Quercus* recruitment in *P. halepensis* stands, a general response curve is shown (grey dotted line).

Environmental and structural characteristics of pine forests

Differences between the two forest types (planted versus natural) as regards ecological conditions – chiefly climatic, edaphic and disturbance regimes – are both causes and consequences of interacting historical, ecological and socio-logical factors. Climatic differences between planted and natural stands are probably due in part to the spatial distribution of planted forests (Fig. 1). Species selection in pine plantations was often guided by edapho-climatic suitability models (see Gandullo & Sánchez-Palomares, 1994), but

was also highly influenced by the historical spatial patterns of deforestation and afforestation in the Iberian Peninsula (e.g. Bauer, 1980). Furthermore, the fact that control of erosion was one of the main reasons underlying the reforestation of many degraded areas could explain why some planted pine forests are currently located on poorer soils (rockier and more acidic soils).

The higher intensity of perturbations (anthropic mortality and fire) found in planted with respect to natural pine forests could be related to timber production and structural stand characteristics such as high-density, even-aged structure and horizontal homogeneity (Lloret *et al.*, 2002). Widespread high

Table 3 Best models of woody species richness in stands of the five pine species studied. The selected transformation (*poly* (2) is polynomial transformation of order 2), degrees of freedom (d.f.), model deviance (M. Dev.), deviance (Dev.) and probabilities of chi-square tests of the effect of the variable are given.

	<i>Pinus halepensis</i> (M. Dev.: 0.35)			<i>Pinus pinea</i> (M. Dev.: 0.49)			<i>Pinus pinaster</i> (M. Dev.: 0.28)			<i>Pinus nigra</i> (M. Dev.: 0.36)			<i>Pinus sylvestris</i> (M. Dev.: 0.51)		
	d.f.	Dev.	$P(\chi^2)$	d.f.	Dev.	$P(\chi^2)$	d.f.	Dev.	$P(\chi^2)$	d.f.	Dev.	$P(\chi^2)$	d.f.	Dev.	$P(\chi^2)$
Forest type	1	1440	< 0.0001	1	105.6	< 0.0001	1	2.3	0.1264	1	516.8	< 0.0001	1	991.3	< 0.0001
Temperature <i>poly</i> (2)	2	170.1	< 0.0001	2	727.5	< 0.0001	2	803.2	< 0.0001	2	1448.1	< 0.0001	2	5190.2	< 0.0001
Precipitation <i>poly</i> (2)	2	2557.2	< 0.0001	2	680.9	< 0.0001	2	208	< 0.0001	2	197.1	< 0.0001	2	130.1	< 0.0001
Soil rockiness	2	19.5	< 0.0001				2	232.3	< 0.0001	2	51.1	< 0.0001	2	49.2	< 0.0001
Soil texture	2	124.8	< 0.0001	2	136	< 0.0001	2	309.5	< 0.0001	2	24.1	< 0.0001	2	253.2	< 0.0001
Soil pH	2	19.9	< 0.0001	2	120.9	< 0.0001	2	293.5	< 0.0001	2	26.1	< 0.0001	2	171.2	< 0.0001
Basal area <i>poly</i> (2)	2	57.4	< 0.0001	2	32.5	< 0.0001	2	71.7	< 0.0001	2	67.1	< 0.0001	2	74.1	< 0.0001
Tree dens. <i>poly</i> (2)				2	101	< 0.0001	2	98.7	< 0.0001				2	20.3	< 0.0001
CVd <i>poly</i> (2)	2	61.3	< 0.0001	2	70.4	< 0.0001	2	246.6	< 0.0001	2	76.7	< 0.0001	2	131.4	< 0.0001
Monosp. <i>poly</i> (2)	2	218.3	< 0.0001	2	197	< 0.0001	2	507.2	< 0.0001	2	73.3	< 0.0001	2	249.9	< 0.0001
Nat. mor. <i>poly</i> (2)	2	9.1	0.0108				2	7.6	0.0226				2	41.8	< 0.0001
Ant. mor. <i>poly</i> (2)							2	4.3	0.1176						
Road <i>poly</i> (2)	2	59.9	< 0.0001	2	46.5	< 0.0001	2	0.3	0.8630	2	50.3	< 0.0001	2	98.1	< 0.0001
Fire <i>poly</i> (2)	2	306.2	< 0.0001	2	100.3	< 0.0001	2	90	< 0.0001	2	122.2	< 0.0001	2	138.5	< 0.0001
Protection										1	36.3	< 0.0001			

Temperature: mean annual temperature; Precipitation: annual precipitation; Basal area: basal area ($\text{m}^2 \text{ha}^{-1}$); Tree dens.: tree density (trees per ha); CVd: coefficient of variation of tree diameter; Monosp.: monospecific character (%); Nat. mor.: basal area lost by natural mortality ($\text{m}^2 \text{ha}^{-1}$); Ant. mor.: basal area lost by anthropic mortality ($\text{m}^2 \text{ha}^{-1}$); Road: distance to road (m); Fire: fire frequency; Protection: protected area. Differences were considered significant at $P(\chi^2) < 0.05$ and are marked in bold.

pine stand densities in Spain might be due both to initial planting densities and lack of post-silvicultural operations (Madrigal, 1998). Thus, a combination of edapho-climatic conditions, structural characteristics and disturbance regimes may lead to differences in the patterns of recruitment and woody species richness between the two forest communities.

Seedling recruitment patterns

In general, pine plantations exhibited lower seedling abundance than natural pine stands, and this effect was more pronounced for oak regeneration. The maximum seedling abundance and the largest differences between forest types were generally found at mesic (medium precipitation) sites, intermediate stand densities, low fire frequencies and in stands closer to *Quercus* forests.

Oak regeneration is influenced by multiple factors operating at different ontogenetic stages, from fecundity (Espelta *et al.*, 1995; Pérez-Ramos *et al.*, 2010) and seed supply (García *et al.*, 2010) to germination, emergence and establishment of oak seedlings (Gómez *et al.*, 2004; Mendoza *et al.*, 2009). The ecological gradients examined in this study may be interpreted as correlates of underlying mechanisms driving these processes; distance to the nearest *Quercus* forest with seed supply (Gómez-Aparicio *et al.*, 2009); precipitation and tree density gradients with seed and seedling responses to light and water availability (Rey Benayas *et al.*, 2005; Urbietta *et al.*, 2010); and fire frequency with disturbance regimes (Richardson *et al.*, 2007). Oak recruitment was largely affected by distance to seed

sources, especially in Mediterranean pine forests (Table 2), suggesting that the regeneration process is seed limited (e.g. Purves *et al.*, 2007; Zamora *et al.*, 2010). Long-distance dispersal events are crucial for plant colonization and persistence (Cain *et al.*, 2000) and seed arrival at planted forests may be retarded. Firstly, average distances between pine stands and the nearest *Quercus* forest (Table 1) were much further than the maximum dispersal distance reported for the European jay, *Garrulus glandarius*, the main disperser of acorns in Mediterranean forests (e.g. Gómez, 2003; Pons & Pausas, 2007). Moreover, the relatively more homogeneous structure of pine plantations relative to natural stands (Table 1) may lead to a lower avian abundance and thus to a lower seed supply (López & Moro, 1997; Zamora *et al.*, 2010).

The observed correlation of precipitation and tree density with seedling recruitment – hump-shaped pattern – may reflect various mechanisms associated with resource availability and stress conditions. Specifically, water and light availability exert a critical effect on regeneration in Mediterranean forests (i.e. Marañón *et al.*, 2008; Quero *et al.*, 2011). Seedling establishment can be limited under stressful conditions of both water scarcity (Maestre & Cortina, 2004) and overabundance (Urbietta *et al.*, 2008). A number of studies have reported optimal conditions for successful oak establishment and growth at intermediate precipitation and stand density values (e.g. Lookingbill & Zavala, 2000). Specially, oak seed germination and seedling establishment can benefit from partial cover because of water stress reduction (Espelta *et al.*, 1995; Siles *et al.*, 2010). However, at higher densities, light can

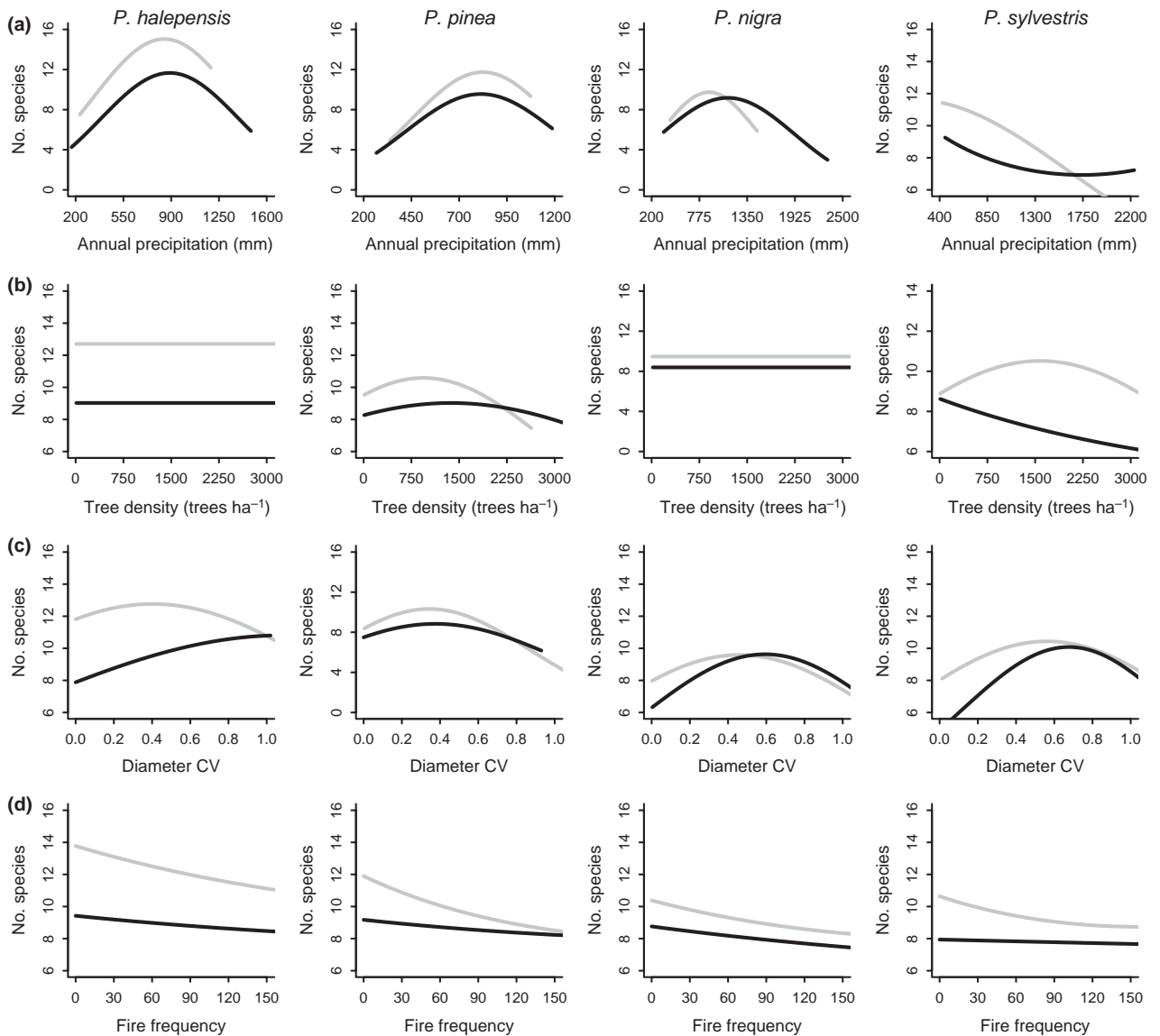


Figure 4 Form of the relationships between predicted woody species richness along annual precipitation (a); tree density (b); coefficient of variation of tree diameter (c); and fire frequency (d) in planted (black line) and natural (grey line) forest stands of *Pinus halepensis*, *Pinus pinea*, *Pinus nigra* and *Pinus sylvestris*. *Pinus pinaster* was not considered in this analysis because forest type had a non-significant effect on woody species richness. Interactions significant between forest type and environmental variables are available in Table S2, and straight lines denote a non-significant effect of the variable on recruitment and are shown in these figures only for comparative purposes.

become a limiting factor, inducing a recruitment bottleneck in Mediterranean oak tree species (Zavala *et al.*, 2011). In mountain pine forests, however, a lower productivity (Pausas & Austin, 2001) and higher understorey light levels may preclude oak mortality under pine stands.

Frequent fires caused a strong decrease in oak seedling abundance, especially pronounced in mountain pine ecosystems (Fig. 3d). The ability of oaks to withstand fires (i.e. through resprouting) is controversial and depends on the frequency and intensity of the fire regime (see López-Soria & Castell, 1992; Pausas *et al.*, 2008). The decrease in oak recruitment may also be directly linked to the loss of vegetation cover, altering oak seed supply and establishment (García

et al., 2010). In spite of the decrease observed in oak seedling abundance, oak recruitment was higher than pine recruitment along the entire fire frequency gradient. Previous studies have reported negative effects of intense and frequent fires on mountain pine recruitment, observed to a lesser extent for oak recruitment (Espelta *et al.*, 2002; Rodrigo *et al.*, 2007).

Woody species richness patterns

In agreement with Pausas & Austin (2001), we found that diversity was primarily driven by climate and stand structure, while disturbances played a secondary but important role. Differences in species richness between the two forest types

were not constant and changed along ecological gradients, being more pronounced in the gradient sections in which natural forests exhibited maximum richness values. Specifically, this pattern was observed for gradients of precipitation, stand structure (tree density and stand evenness) and fire frequency.

Species richness showed a hump-shaped pattern along the precipitation gradient in all stands except those of *P. sylvestris*, where it followed an exponential decay (Fig. 4a). A humped-shaped relationship between species richness and resource availability (e.g. precipitation as a proxy for water availability) has frequently been reported (e.g. Pausas & Austin, 2001). However, high precipitation levels in Iberian alpine environments are usually related to high elevation and cold areas, which might explain the unusual negative correlation between precipitation and richness observed in *P. sylvestris* stands (Rey Benayas & Scheiner, 2002).

Structural complexity promotes diversity through various mechanisms associated with resource variability and habitat heterogeneity (see Carnus *et al.*, 2006; Quilchano *et al.*, 2008). Accordingly, woody species richness followed a hump-shaped relationship with respect to a gradient in structural heterogeneity (i.e. tree density and stand evenness). Other studies have also reported a link between the simplified structure of plantations and their lower levels of plant diversity (Lindenmayer & Hobbs, 2004; Bremer & Farley, 2010). It is well known that horizontal and vertical stand heterogeneity have a positive effect on plant species diversity (Halpern & Spies, 1995; Brockerhoff *et al.*, 2008) and this effect has previously been reported in woody species richness under pine forests (Pausas, 1994). This heterogeneity also influences seed disperser preferences and can therefore contribute to the abundance and composition of the seed rain within the pine plantation (Zamora *et al.*, 2010).

Fire frequency exerted a negative influence on woody species richness with decreasing richness values at higher frequencies for both planted and natural forests. Thus, we did not find support for the Intermediate Disturbance Hypothesis (IDH, Connell, 1978), see Fig. 4, which predicts that maximum species richness occurs at an intermediate level of perturbation. The IDH remains, however, controversial (Miller *et al.*, 2011), and our results agree with Collins *et al.* (1995), who found a negative relationship between species richness and fire frequency.

Insights for management of Mediterranean planted pine forests

Our results suggest that some planted pine forests were established beyond the natural climatic range for pine forests in Spain and that the structural characteristics of planted stands differ markedly with respect to natural forests. These differences are translated into lower tree regeneration and woody species diversity along large parts of the environmental gradients explored. Based on our multivariate analyses, we propose a set of priorities to guide current planted pine forests

towards a more natural state in areas where recovery of structure and functionality is feasible.

Firstly, we suggest that management activities should target those planted forests that differed from the structure of natural rich pine forests. Specifically, this includes plantations with high tree density, a low coefficient of variation of tree diameter and high monoespecificity. Some of these attributes are a result of initial plantation density, but most result from a lack of post-plantation operations because of socioeconomic factors (Madrigal, 1998). Thinning would be highly recommended in such plantations to increase their structural heterogeneity. A higher structural heterogeneity may in turn reduce recruitment limitation by increasing seed supply (e.g. improving bird abundance, Mendoza *et al.*, 2009; Zamora *et al.*, 2010) and promoting favourable microclimatic conditions that may facilitate oak establishment (i.e. higher light availability and lower water stress, Lookingbill & Zavala, 2000; Plieninger *et al.*, 2010). Moreover, high monoespecificity could contribute to decrease the risk of plantation decline (Moreno-Gutiérrez *et al.*, 2011) and fire occurrence (Lloret *et al.*, 2002; Pausas *et al.*, 2004), and increase forest resilience to climatic changes (e.g. Seppälä *et al.*, 2009).

Secondly, we propose that enrichment planting should be considered as a direct way to enhance regeneration and diversity. Enrichment planting should target plantations located in the parts of the gradients where largest differences in recruitment with respect to natural forests occurred (e.g. intermediate tree density, mesic areas), and that happened to coincide with those parts where maximum recruitment values in natural stands were found. These plantations have the greatest potential for successful recruitment of oak species and successional trajectories towards more natural and diverse mixed forests (Zavala *et al.*, 2000).

Finally, plantations of mountain pines (*P. sylvestris* and *P. nigra*) should be prioritized, because they exhibited the strongest divergence in recruitment and diversity with respect to natural pine forests. Moreover, these pine species are particularly vulnerable to potential climatic change (Benito-Garzón *et al.*, 2008; Galiano *et al.*, 2010) and intense fires (Rodrigo *et al.*, 2004; Pausas *et al.*, 2008), which highlights the importance of a quick redirection in management practices to foster resilience.

Pine forests have been present in Iberian landscapes throughout the Holocene, coexisting and alternating with hardwoods and other conifers (e.g. Carrión & Leroy, 2010). Over the last centuries Euromediterranean countries have undergone dramatic changes, including extensive afforestation, but also more recently agricultural land abandonment (Barbero *et al.*, 1998). This has resulted in a spatially complex successional vegetation framework with multiple pathways determined by ecological conditions, management practices and historical contingencies (e.g. Blondel & Aronson, 1995). While natural pine forests can be a useful reference system to guide naturalization of planted pine forests, novel successional trajectories are also likely to take place. For example, pine stands from genetic provenances different from local sources

may exhibit divergent responses along succession or under climate change than locally adapted populations (e.g. Benito-Garzón *et al.*, 2011). Thus, as argued by Hobbs *et al.* (2006), in addition to a reference system-based approach, further work is needed to revise restoration norms and practices that complement the traditional focus on existing or historical assemblages.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Table S1 Mean values and standard error of *Pinus* and *Quercus* seedling abundance for planted and natural forest types of the five pine species studied.

Table S2 Interactions between forest type and all other variables included in the best models for *Pinus* and *Quercus* seedling abundance.

Table S3 Mean values and standard error of woody species richness for planted and natural forest types of the five pine species studied.

Table S4 Interactions between forest type and all other variables included in the best model of species richness.

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BIOSKETCHES

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