

Assessing regional species pools for restoration programs in Spain

José M. García del Barrio · Francisco Auñón · David Sánchez de Ron · Ricardo Alía

Received: 15 November 2011 / Accepted: 23 January 2013
© Springer Science+Business Media Dordrecht 2013

Abstract The relationship between current and potential distribution in 34 main Spanish forest tree species (data from the Third Spanish Forest Inventory) was determined using a Maximum Entropy functional approximation with climatic data as predictive variables. A method for detecting regional species pools at two different scales: biogeoclimatic classes (CLATERES classification), and forest landscape types (WWF classification) has been proposed. Then, the Absence percentage for a species (i.e. the proportion of landscapes types or biogeoclimatic classes in which the species is included in the regional species pool but is actually not present) was determined. Results show higher figures of Potential Species Richness in the Pyrenees and the Cantabrian Range, while inland or coastal Mediterranean semi-arid landscapes have lower figures. Using a classification based on biogeoclimatic variables (CLATERES) improves precision when estimating Absent Species Richness. Absence percentage is zero or close to zero for five species (*Pinus uncinata*, *Quercus robur*, *Quercus ilex*, *Quercus humilis* and *Juniperus communis*), while for other six species (*Acer pseudoplatanus*, *Fraxinus angustifolia*, *Alnus glutinosa*, *Populus alba*, *Sorbus aucuparia* and *Pinus pinea*) the figures are higher than 0.6, which means the species is absent in more than 60 % of the landscapes or biogeoclimatic classes that it could inhabit. The relationships between tree life traits and the absence of species from the ecosystems studied is slight but non-dominant species, species not subjected to

Electronic supplementary material The online version of this article (doi:[10.1007/s11056-013-9363-y](https://doi.org/10.1007/s11056-013-9363-y)) contains supplementary material, which is available to authorized users.

J. M. García del Barrio (✉) · F. Auñón · D. Sánchez de Ron · R. Alía
Dpto. Ecology and Forest Genetics, INIA, Forest Research Centre, Avda. A Coruña km 7.5,
28040 Madrid, Spain
e-mail: jmgarcia@inia.es

J. M. García del Barrio · R. Alía
Sustainable Forest Management Research Institute, UVA-INIA, Avda A Coruña km 7.5,
28040 Madrid, Spain

forest management, or zonal species are less widely distributed than their climatic potentiality indicates.

Keywords Tree species richness · Biogeoclimatic classification of Spain · Absent species · Spanish forest landscapes types · Regional restoration programs

Introduction

One of the main questions when addressing restoration programs is the definition of a species pool, i.e. the set of species that can potentially inhabit a site because of suitable local ecological conditions (Zobel et al. 1998; Holmes and Richardson 1999; Brudvig and Mabry 2008; Kadoya et al. 2008), and the restoration gene pool within those species that can be applied (Jones and Monaco 2009). According to the basic principles of restoration ecology and the recommendations for afforestation and restoration programs (SER 2004), local species should be promoted in most occasions (MCPFE 2007). Additionally, an ecosystem-oriented approach should also benefit from plant species diversification and a better use of the larger available pool of native species (Vallejo 2010). Knowledge of the regional species pool expands restoration possibilities, especially in degraded ecosystems, as the presence of tree species' could be influenced by disturbance regimes, mainly human land uses (as in the Mediterranean region, Rodríguez-Sánchez et al. 2010).

How can a species pool for restoring forest landscapes or regions be estimated? Experimental approaches based on the study of local species pools have been widely used for restoration purposes at the community level (Zobel et al. 1998). Additionally, some ecological, functional, and phytosociological approaches provide information to include species not directly observed but belonging to the regional species pool.

Niche modeling is a functional approach that is especially useful if species presence/absence information is available, because it improves the predictive power of the presence data (Stockwell and Peterson 2002). Niche modeling provides habitat prediction for many species, both in present and future climatic conditions (e.g. Miller and Knouft 2006; Brown et al. 2008; Williams et al. 2009; Blach-Overgaard et al. 2010; Soria-Auza et al. 2010). Several methods for niche modeling have been used: envelope methods (BIOLIM), multivariate distance (DOMAIN), generalized linear (GLMs) or generalized additive models (GAMs), maximum entropy models (MaxEnt), or boosted regression trees (BRT) (Guisan and Thuiller 2005; Elith et al. 2006; Guisan et al. 2007). Among them, maximum entropy models, introduced by Jaynes (1957), have been widely applied in many studies on species diversity (Levich 2000; Pueyo 2006; Shipley et al. 2006; Pueyo et al. 2007).

All these methods are climatic dependent but also influenced by a species' intrinsic ecological characteristics (see Hanspach et al. 2010), which are not always sufficiently known, at least at the scale required in restoration programs. Climatic data have been widely used for modeling patterns of species abundance and distribution (e.g. Ferrer-Castán and Vetaas 2005; Thuiller et al. 2006 or Svenning and Skov 2007). Geological data (e.g. Enright et al. 1994; Austin et al. 1996; Ohmann and Spies 1998) and soil nutritional variables (e.g. Coudun et al. 2006) may improve the performance of fine-scale tree species distribution models. However, this type of information is not so widely available at the regional level.

A central issue when defining a species pool is the geographical scale to which the concept is applied, because the number of species is scale-dependent, according to the

habitat diversity hypothesis (Williams 1964). Different scales would include different degrees of heterogeneity and, specifically, broader scales would merge different environmental conditions (Scott et al. 2011). For example, an aggregation based on a given grid size (e.g. $10 \times 10 \text{ km}^2$) allows an estimation not dependent on size, but would be influenced by administrative boundaries or niche heterogeneity. An ecosystem or landscape typology approach would allow the definition of a species pool with a community meaning, but with different extension of the landscape types. Niche heterogeneity could be minimized if methods for estimating the species pool were to be based on biogeoclimatic regions (Bunce et al. 1996; Elena-Rosselló 1997; Bunce et al. 2002; Ortega et al. 2012).

The hypothesis of this paper is that the “actual species pool”, i.e. the species observed in a given territory, underestimates the species pool for landscape restoration programs in areas under ancient anthropogenic influence.

This hypothesis was contrasted in Peninsular Spain and the Balearic Islands, both of which present high levels of diversity both in vascular plants and tree species (Médail and Quézel 1999). This territory has been considered as a Pleistocene refuge, and its present vegetation is a result of land uses, interaction with forest fires, floods, and drier climate periods (Bolle 2003). All these factors make Spain an excellent model for exploring the relationship between current and potential species richness in order to assess the importance of the absent species in establishing a species pool for landscape restoration programs.

The aims of the paper are: (a) to provide a method to estimate the species pool for landscape restoration or afforestation programs at two territorial scales with different biological meaning (biogeoclimatic classes, and forest landscape types), (b) to test the validity of the method for the different species by analyzing the relationships among different life history traits, and their observed and potential presence. Data on the pseudopresence of the species are derived from the Third National Forest Inventory (Villanueva 2004). We combine the use of extensive databases, easily accessible for many countries, with niche modeling approaches based on a MaxEnt prediction (Phillips et al. 2004; Phillips et al. 2006), for estimating observed and predicted species richness, and also for calculating the species restoration pool, taking into account the regional species pool for biogeoclimatic classes (Elena-Rosselló 1997) or forest landscape types (WWF 2009; Sainz-Ollero et al. 2010).

Material and Methods

We analyzed 40 native forest tree species in Peninsular Spain and the Balearic Islands. The species belong to the genera *Abies* (2 species), *Acer* (1), *Alnus* (1), *Arbutus* (1), *Betula* (2), *Castanea* (1), *Fagus* (1), *Fraxinus* (2), *Ilex* (1), *Juniperus* (4), *Olea* (1), *Pinus* (6), *Populus* (3), *Quercus* (9), *Sorbus* (2), *Tamarix* (1), *Tilia* (1) and *Ulmus* (1), (Table 1). These native species are the most commonly used in afforestation, restoration, and conservation programs in Spain, as stated by the Spanish Strategy for Conservation and Sustainable Use of Forest Genetic Resources (Jimenez et al. 2009), and they are regulated in Spain according to EU Directive on the marketing of forest reproductive material (CE 1999).

The species were classified (Table 2) according to different traits (Ruiz de la Torre 2006; Alía et al. 2009): RLUC- Ratio of estimated distribution not affected by induced human land use change. It is obtained as the ratio of predicted distribution area of the species in forested area in respect to the total predicted area of the species (i.e. including forested, urban, and other non-forestry land uses)-, CI-Climatic (M: Mediterranean species,

Table 1 Summary of the 34 Spanish forest tree species selected from the MaxEnt niche modelling (see variables names in the text)

Species	Maxent-Th	Training points	AUC	AT	Variable Percent contribution									
					MLTCM	MHTWM	AR	SR	FR	WR	ND_5 °C	NDD	EL	
<i>Abies alba</i>	0.363	1,339	0.994	13.9	0.3	3	0.1	56.7	0.1	1	15.6	8.6	0.8	
<i>A. pinsapo</i>	0.382	136	0.999	0.1	0.8	0.6	0.4	28.7	10.2	39.8	0.2	3.7	15.5	
<i>Acer pseudoplatanus</i>	0.275	900	0.958	1.6	3.4	7.8	35.4	39.9	0.2	1.4	0.9	1.7	7.8	
<i>Alnus glutinosa</i>	0.202	4,686	0.893	4.4	2.3	8.7	43.5	7.9	8	3.3	0.3	0.9	20.8	
<i>Arbutus unedo</i>	0.263	7,833	0.894	13.8	2.3	5.8	15	9.5	29.6	2.6	10.4	2.6	8.3	
<i>Betula alba</i>	0.321	5,344	0.954	4.1	0.6	15.5	68.2	6.3	0.1	1.1	2.2	0.1	1.8	
<i>Castanea sativa</i>	0.316	8,290	0.934	3.5	0.9	3.3	44.8	3	25	3.5	13.3	0.4	2.3	
<i>Fagus sylvatica</i>	0.405	19,344	0.965	3.7	2.1	29.1	4.6	54.5	0.6	1.8	0.6	0.6	2.5	
<i>Fraxinus angustifolia</i>	0.267	5,344	0.781	1.8	19.2	11	9.6	12.2	7.1	24.8	0.9	0.3	13.1	
<i>F. excelsior</i>	0.221	2,596	0.96	0.8	1.6	6.3	5.9	77.7	2.2	1.3	1.4	0.2	2.5	
<i>Ilex aquifolium</i>	0.295	5,081	0.941	1.3	2.2	4.7	16.9	69.4	0.3	0.9	0.3	0.5	3.6	
<i>Juniperus communis</i>	0.29	9,237	0.92	0.4	3.4	3.1	6.7	53.5	0.6	8.9	19.2	3.6	0.7	
<i>J. oxycedrus</i>	0.265	10,369	0.842	16.6	1.2	12.7	2	16.2	23.5	20.4	0.7	1.6	5	
<i>J. phoenicea</i>	0.272	4,878	0.87	2.4	6.4	22.1	6	10.3	10.4	31.8	0.6	2.1	8	
<i>J. thurifera</i>	0.296	14,502	0.933	2.1	9.5	5.5	0.5	22	9.9	1.7	1.6	3.1	44	
<i>Olea europaea</i>	0.337	11,447	0.893	42.5	15.2	9.4	1.8	2.9	21.1	1.6	0.1	2.3	3	
<i>Pinus halepensis</i>	0.318	54,193	0.878	23	23.2	4.5	9.3	5.1	4.6	22.9	2.4	2.1	3	
<i>P. nigra</i>	0.302	20,532	0.944	29.3	6.6	6.1	0.5	10.5	29.2	3.1	2.1	0.7	11.8	
<i>P. pinaster</i>	0.249	16,231	0.877	8.6	3.6	15	6.5	20.6	3.2	8.2	1.1	2.7	30.5	
<i>P. pinea</i>	0.365	9,818	0.907	11.8	7.1	6.6	16.1	20.3	4.2	8.3	1	6.6	18	
<i>P. sylvestris</i>	0.423	20,824	0.959	0.9	10.7	3.6	3.6	54.3	4	6	10.4	5.7	0.9	
<i>P. uncinata</i>	0.245	3,640	0.994	0.5	41.1	2.2	0.4	45.5	0	0.6	2.4	5.7	1.5	
<i>Populus alba</i>	0.245	9,015	0.822	2.1	10.6	11.9	4.9	9.1	28.9	4.6	1.7	0.9	25.4	
<i>P. nigra</i>	0.354	31,824	0.743	2.3	37.5	9.4	13.2	12.7	4.7	3.4	0.7	5	11	

Table 1 continued

Species	Maxent-Th	Training points	AUC	AT	Variable Percent contribution									
					MLTCM	MHTWM	AR	SR	FR	WR	ND_5 °C	NDD	EL	
<i>Quercus canariensis</i>	0.228	692	0.994	2.4	13.2	9.4	30.7	21.3	0.2	19.1	0.4	0.9	2.3	
<i>Q. faginea</i>	0.36	53,281	0.84	1.7	25.5	4.6	24	6.3	0.9	11.2	16.3	0.4	9	
<i>Q. humilis</i>	0.375	10,174	0.977	0.8	2.6	6	1.2	69.5	4.6	11.8	1.4	0.6	1.5	
<i>Q. ilex</i>	0.434	182,023	0.71	9.4	10	9.6	49.2	5.3	0.5	5.5	1.8	0.3	8.3	
<i>Q. petraea</i>	0.334	9,734	0.964	3.3	8.2	2	20.7	58.9	0.6	0.6	1.6	1.4	2.8	
<i>Q. pyrenaica</i>	0.394	49,141	0.901	12	15.9	0.7	22.7	18.8	0.8	24.4	0.9	0.8	3	
<i>Q. robur</i>	0.461	32,076	0.956	0.2	1.7	0.8	75.1	9	0	5.6	0.2	1.6	5.7	
<i>Q. suber</i>	0.322	26,776	0.916	38.9	1.5	6.3	28.7	0.8	5	14.7	0.2	1.6	2.4	
<i>Sorbus aria</i>	0.236	2,590	0.954	10.2	0.2	1.3	16.2	52.8	1.3	2.5	9.9	0.7	4.8	
<i>S. aucuparia</i>	0.232	2,196	0.946	8.6	3	1.5	0.6	56.9	10.7	1.4	7.5	6.6	3.2	

Table 2 Relationship between variables species distribution at $1 \times 1 \text{ km}^2$ grid and species life traits (see variables names in the text)

Species	P	O	PR	OR	EF	% OPN	RLUC	CI	Do	Di	Ec	SFM
<i>Abies alba</i>	8,994	1,339	85.3	13.7	1.1	7.17	97.61	NM	0	1	0	0
<i>A. pinsapo</i>	1,163	136	88.4	10.6	1.0	8.82	100.0	M	0	1	0	1
<i>Acer pseudoplatanus</i>	50,642	900	98.2	1.6	0.2	11.67	91.11	NM	1	1	0	1
<i>Alnus glutinosa</i>	89,050	4,687	94.8	4.2	1.0	19.78	75.40	NM	1	1	1	1
<i>Arbutus unedo</i>	120,611	7,837	93.6	5.6	0.8	12.82	95.90	M	1	2	0	1
<i>Betula alba</i>	55,710	5,344	90.5	8.7	0.8	8.91	89.30	NM	1	1	0	1
<i>Castanea sativa</i>	69,947	8,301	88.3	10.6	1.1	9.35	90.07	NM	0	2	0	0
<i>Fagus sylvatica</i>	50,845	19,344	62.7	35.4	1.9	5.15	94.64	NM	0	2	0	0
<i>Fraxinus angustifolia</i>	254,848	5,344	97.9	1.8	0.3	13.92	69.63	M	0	1	1	1
<i>F. excelsior</i>	41,236	2,596	93.8	5.4	0.8	13.60	92.37	NM	1	1	0	1
<i>Ilex aquifolium</i>	70,586	5,081	92.9	6.4	0.7	10.37	97.11	NM	1	2	0	1
<i>Juniperus communis</i>	95,402	9,237	90.4	8.6	1.0	10.59	93.85	NM	1	2	0	1
<i>J. oxycedrus</i>	173,508	10,377	94.1	5.2	0.8	12.89	88.65	M	1	2	0	1
<i>J. phoenicea</i>	150,953	4,917	96.8	2.8	0.4	12.67	86.68	M	1	2	0	1
<i>J. thurifera</i>	77,261	14,502	81.6	16.5	1.9	10.22	75.60	M	0	2	0	1
<i>Olea europaea</i>	130,033	11,504	91.3	7.6	1.2	13.33	71.59	M	1	2	0	1
<i>Pinus halepensis</i>	180,050	54,294	70.5	27.3	2.2	7.37	63.82	M	0	1	0	1
<i>P. nigra</i>	69,999	20,532	71.3	26.6	2.1	7.26	86.54	NM	0	1	0	0
<i>P. pinaster</i>	183,822	38,600	80.5	12.3	7.2	37.09	73.77	M	0	1	0	0
<i>P. pinea</i>	118,160	9,841	91.8	7.0	1.2	14.51	65.58	M	0	2	0	0
<i>P. sylvestris</i>	54,973	20,824	63.0	34.7	2.3	6.15	91.87	NM	0	1	0	0
<i>P. uncinata</i>	7,998	3,640	55.3	42.9	1.8	3.96	97.47	NM	0	1	0	1
<i>Populus alba</i>	200,470	9,015	95.5	3.8	0.6	14.27	35.78	NM	0	1	1	0
<i>P. nigra</i>	342,436	31,824	90.8	8.7	0.5	5.66	52.79	NM	0	1	1	0
<i>Quercus canariensis</i>	4,394	694	84.5	13.8	1.7	11.24	92.51	M	1	2	0	1
<i>Q. faginea</i>	211,948	53,282	75.3	23.0	1.7	6.86	74.77	M	0	2	0	0

Table 2 continued

Species	P	O	PR	OR	EF	% OPN	RLUC	CI	Do	Di	Ec	SFM
<i>Q. humilis</i>	31,027	10,174	67.8	30.5	1.7	5.31	78.67	NM	1	2	0	1
<i>Q. ilex</i>	410,653	182,082	55.9	43.5	0.6	1.35	72.48	M	0	2	0	0
<i>Q. petraea</i>	47,164	9,734	79.7	18.6	1.7	8.31	91.21	NM	0	2	0	0
<i>Q. pyrenaica</i>	136,606	49,141	64.8	32.9	2.3	6.41	83.20	M	0	2	0	0
<i>Q. robur</i>	54,320	32,111	42.0	56.0	2.0	3.40	74.85	NM	0	2	0	0
<i>Q. suber</i>	104,629	26,785	75.0	22.8	2.3	9.00	85.68	M	0	2	0	0
<i>Sorbus aria</i>	48,999	2,590	94.8	4.5	0.7	13.86	98.07	NM	1	2	0	1
<i>S. aucuparia</i>	56,085	2,196	96.1	3.3	0.6	15.16	98.27	NM	1	2	0	1

NM: non Mediterranean species), Do-Dominance (0: dominant species, 1: secondary species), Di-Dispersal (1: anemochorous, 2: zoo/autochorous, 3: other), Ec-Ecology (0: zonal species, 1: azonal species), and SFM—Subject to Forest Management (1: Subjected to Forest Management, 0: Not Subjected to Forest Management).

Observed and Predicted species distribution

Distribution data of these 40 forest tree species come from the Third Spanish Forest Inventory (SFI) (Villanueva 2004). Each SFI plot is systematically distributed in a grid of $1 \times 1 \text{ km}^2$ that covers forested areas. Sampling design of each plot includes four concentric circles of radius 5, 10, 15, and 25 m. A complete list of tree species observed, UTM coordinates, and elevation (m) are available for each SFI sampled plot. Information from the Spanish Forestry Map at scale 1:50.000—MFE50—(MMA 2002) was also used to complete the distribution of the species by overlapping the list of species in each map patch with the $1 \times 1 \text{ km}^2$ grid-plot, and adding non recorded species to the corresponding SFI plot. We excluded non autochthonous populations of the species (see Alia et al. 2009). Therefore, presence/absence data of each species was obtained for each SFI grid-plot.

Predicted distribution for each species was obtained by niche modeling using the maximum entropy distribution method (MaxEnt) (Phillips et al. 2004; Phillips et al. 2006) based on nine climatic variables and one topographic variable, elevation (EL). These climatic variables were mean annual temperature (AT), mean daily lowest temperature of the coldest month (MLTCM), mean daily highest temperature of the warmest month (MHTWM), annual rainfall (AR), summer rainfall (SR), fall rainfall (FR), winter rainfall (WP), number of days with mean temperature greater than $5 \text{ }^\circ\text{C}$ (ND_5 $^\circ\text{C}$), and number of days of the drought period (NDD). The values were obtained for each plot using a climatic model (Gonzalo 2010) for Peninsular Spain and the WorldClim database (Hijmans et al. 2004) for the Balearic Islands. No edaphic variables have been introduced as predictors, because there is not at present a digital cartography of soil properties at $1 \times 1 \text{ km}^2$ grid-scale. For each $1 \times 1 \text{ km}^2$ grid-plot the species was considered as *MaxEnt-predicted* when the probability of existence of the species was higher than the threshold value corresponding to the 10 %-percentile (Lth_10 %). We used the Area Under the ROC Curve (AUC) values for evaluating the Maxent predictive distribution models. Not all the variables have had the same influence on each species' distribution as it is shown in Table 1.

Data analysis

The relationship between distribution data and different species life traits was tested. Distribution variables were: observed (O) and Predicted (P) distribution in number of grid-cells, the percentage of grid-cells in which the species is predicted but not observed (Predicted Ratio—PR), the percentage of grid-cells in which the species is predicted and observed (Observed Ratio—OR), the percentage of grid-cells in which the species is observed but not predicted (Error Factor—EF), and the percentage of grid cells in which the species is living out of its potential distribution area (OPN). We have computed the correlation coefficient among those variables (O, P, PR, OR and OPN) and the life history traits (Pearson correlation coefficient with FPA and Spearman Rank Order correlation for the rest of traits).

In order to calculate the regional species pools, we approached at two different scales:

- (a) *Biogeoclimatic classes.* The CLATERES classes (Elena-Rosselló et al. 1997) consist of ecological zones with similar biotic and abiotic factors such as topography, vegetation, and climate. The biogeoclimatic classes vary in extension (mean 2,341 km², with a minimum of 12 and a maximum of 8,939), and in number of patches (mean 43.4, with a minimum of 1 and a maximum of 171). We aggregated the information of predicted and observed richness obtained at the 1 km × 1 km grid cell to each of the 215 CLATERES classes. We included a species within the predicted richness of a given biogeoclimatic class when the predicted distribution is significantly higher than a null random distribution (i.e. the probability is outside the confidence interval of a binomial random distribution), based on the 1 × 1 km² grid.
- (b) *Forest landscape types.* We also aggregated the information of predicted richness for the forest landscapes described in Spain (WWF 2009; Sainz-Ollero et al. 2010)—summarized in Table S1 (Supplementary information) and Figure S1. At present 52 types and subtypes have been described. Thirteen of them are located in the Atlantic climatic zone (forest landscape codes 1 and 2), and the rest (39 forest landscapes) in the Mediterranean one, presenting a wide variation in extension (mean 9,590 km², with a minimum of 83 km², and a maximum of 96,465 km²), number of patches (mean 8.8 with a minimum of 1 and a maximum of 67), and percentage of actual forest land use (mean 67.2 %, with a minimum of 12.5 %, and a maximum of 99.0 %). The description of each forest landscape type and descriptive information is included under Supplementary information (Table S1).

We calculated Predicted Species Richness (PSR), as an estimator of regional species pool, and Observed Species Richness (OSR). Absent Species Richness (ASR) was computed as the difference between PSR and OSR, and Absent Species Ratio (AS) as

$$AS = \frac{2 \times OSR - PSR}{PSR}.$$

AS ratio ranges from -1 (No observed species in the species pool) to 1 (all the potential species are present in the species pool).

Finally, we compute for each species the Absence Percentage (Ap), i.e. the proportion of landscapes types or biogeoclimatic classes in which the species is included in the regional species pool but its actual presence is under 5 % of the total extension. The percentage ranges from 0 (the species is present in all its potential groups) to 100 (the species is absent from all its potential groups).

Results

Results of MaxEnt species distribution models are shown in Table 1, with training data AUC ranging from 0.71 (*Quercus ilex*) to 0.99 (*Abies Pinsapo*), and having 22 out of 34 AUCs values over 0.9. For the subsequent analysis, 6 out of the 40 species were discarded because the AUC in the MaxEnt distribution model was less than expected (*Betula pendula*, *Populus tremula*, *Quercus coccifera*, *Tamarix gallica*, *Tilia platyphyllos* and *Ulmus glabra*).

Rainfall variables (mainly summer and annual rainfall) had a seminal influence in the distribution of many tree species, mainly the non Mediterranean ones (*Fraxinus excelsior*,

Quercus robur, *Acer pseudoplatanus* or *Ilex aquifolium*), or in combination with some temperature variables (*Betula alba*, *Fagus sylvatica* and *Pinus uncinata*). Mediterranean species are related to more than three variables (3.66 ± 0.98), where the most predictive variable is related to temperature for 4 out of 15 species (*Olea europaea*, *Pinus halepensis*, *Quercus faginea* and *Quercus suber*). Finally, elevation is the main variable for two species (*Juniperus thurifera* and *Pinus pinaster*).

The 34 species included in the final analysis display contrasting patterns in a number of predicted and observed $1 \times 1 \text{ km}^2$ grids for each species. Number of grids where a particular species is observed varies from *Q. ilex* (with 182,082 grid cells), to *A. pinsapo* (with 136 grid cells), and the number of grids where a species is predicted varies from *Q. ilex* (410,653 grid cells) to *A. pinsapo* (1163 grid cells).

Species with greater percentages of realized niches (Observed Ratio) are *Q. robur* (56 %), *Q. ilex* (43.5 %), *P. uncinata* (42.9 %), *F. sylvatica* (35.4 %) and *Pinus sylvestris* (34.7 %). On the other hand, 16 out of 34 species have Observed Ratio values lower than 10 % (Table 2). Only three species show values over 15 % in OPN (presence out of the predicted area); *Alnus glutinosa* (19.78 %), *P. pinaster* (37.09 %), and *Sorbus aucuparia* (15.16 %), but 13 out of 34 reach values between 10 and 15 % (Table 2).

Globally, predicted number of grid cells (P) is negatively related to the Ratio of Land Use Change (RLUC, $R = -0.66^{**}$). RLUC is also negatively related to the ecology of the species (Ec, $r = -0.47^{**}$), because the four zonal species studied (Table 2) are located in less forested areas. Percentage of the species living Out of the Predicted Area (OPN) is related to two life trait variables, Dominance (Do, $r = 0.46^{**}$) and Forest Management (SFM, $r = 0.38^*$), which are strongly co-related ($r = 0.74^{**}$). The latter implies that some of the most important managed species have been widely planted out of their original and potential distribution area. There is a significant relationship ($r = 0.44^{**}$) between two life trait variables, dispersion Di and Ecology (Ec), as the four zonal species have anemochorous dispersion; and a slight relationship between another two variables, Climate (Cl) and PFA ($r = -0.35^*$), related to the relatively lower presence of Mediterranean species in massively forested areas.

Values of Observed Species Richness (OSR) and Predicted Species Richness (PSR) at the $1 \times 1 \text{ km}^2$ grid cells are shown in Fig. 1. The scores range from 0 to 11 in relation with OSR (average 1.43 ± 1.45), and from 0 to 23 (average 7.4 ± 3.8) for PSR. Only the north of Spain and the interior mountain ranges show OSR values of over 8 species per grid cell.

Absent Species ratio (AS) for landscape types (AS_l) and biogeoclimatic classes (AS_b) are shown in Fig. 2. Both the greater number of classes (215 versus 52) and the differences between average values for AS_b (0.25 ± 0.4) and AS_l (0.45 ± 0.3) are significant, and indicate that the scale of biogeoclimatic classes is more sensitive for detecting local differences in relation to the species that could be included in the species' restoration pool.

In relation to the species studied, there is a strong correlation ($R = 0.86^{**}$) between Absence percentage (Ap) for species in landscapes types (Ap_l) and biogeoclimatic classes (Ap_b), as could be expected, but there is only a weak correlation between Ap_b and three life trait variables: Do ($r = 0.34^*$), Ec ($r = 0.38^*$) and SFM ($r = 0.36^*$). This indicates that greater species Absence percentages could be found in zonal species, non-dominant at stand level and not subjected to forest management.

There are some species (*P. uncinata*, *Q. robur*, *Q. ilex*, *Quercus humilis* or *Juniperus communis*, see Fig. 3) that are distributed in almost all their potential landscapes or biogeoclimatic classes, but others are absent in more than 60 % of the landscapes or biogeoclimatic classes they could inhabit (*A. pseudoplatanus*, *Fraxinus angustifolia*,

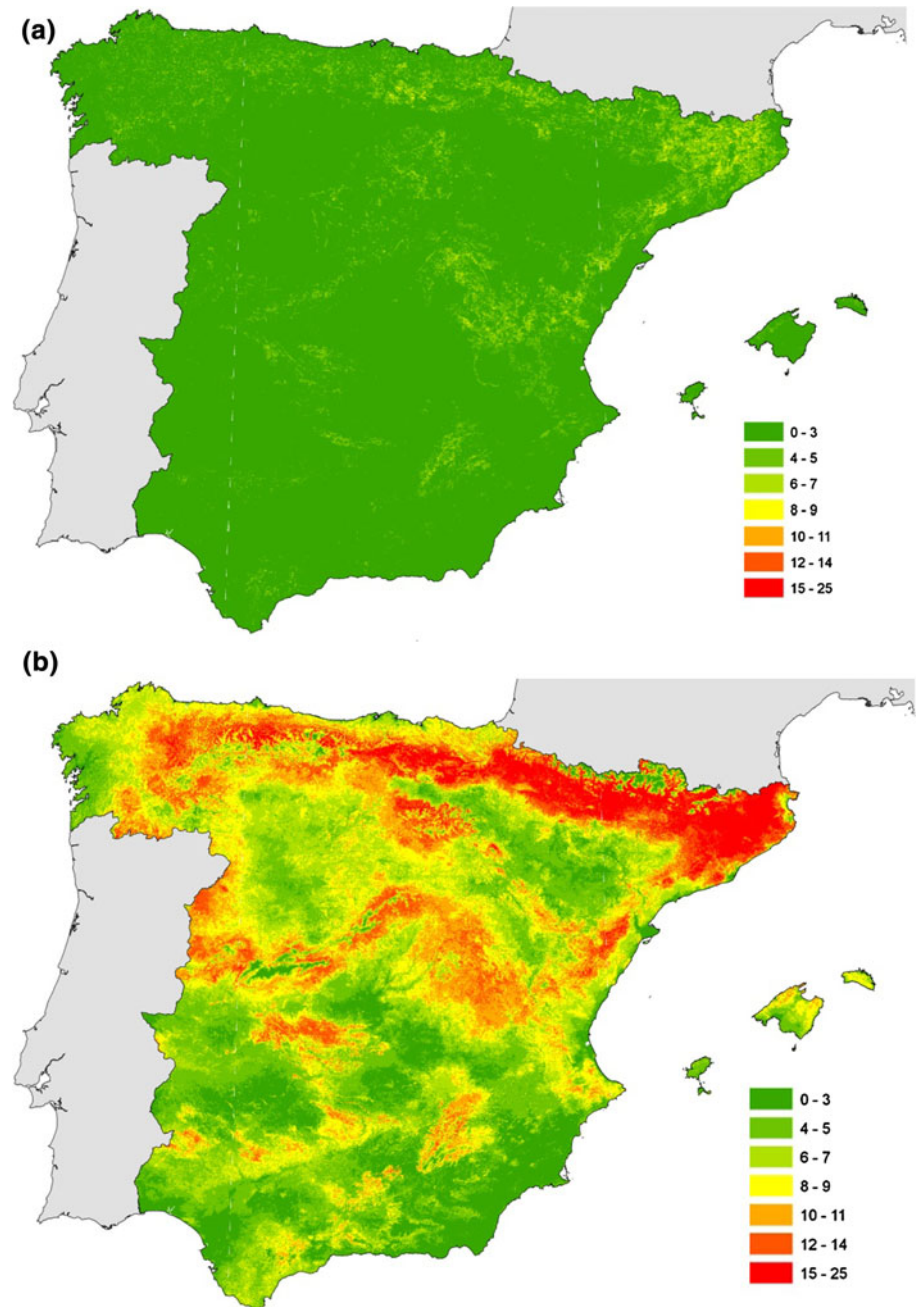


Fig. 1 a Observed species richness (OR) and b Predicted species richness (PR) at $1 \times 1 \text{ km}^2$

A. glutinosa, *Populus alba*, *S. aucuparia* and *Pinus pinea*). *Q. ilex*, for instance, is the most widely distributed species, included in 25 out of 52 landscapes and 119 out of 215 biogeoclimatic classes, being absent only in one potential landscape and one potential

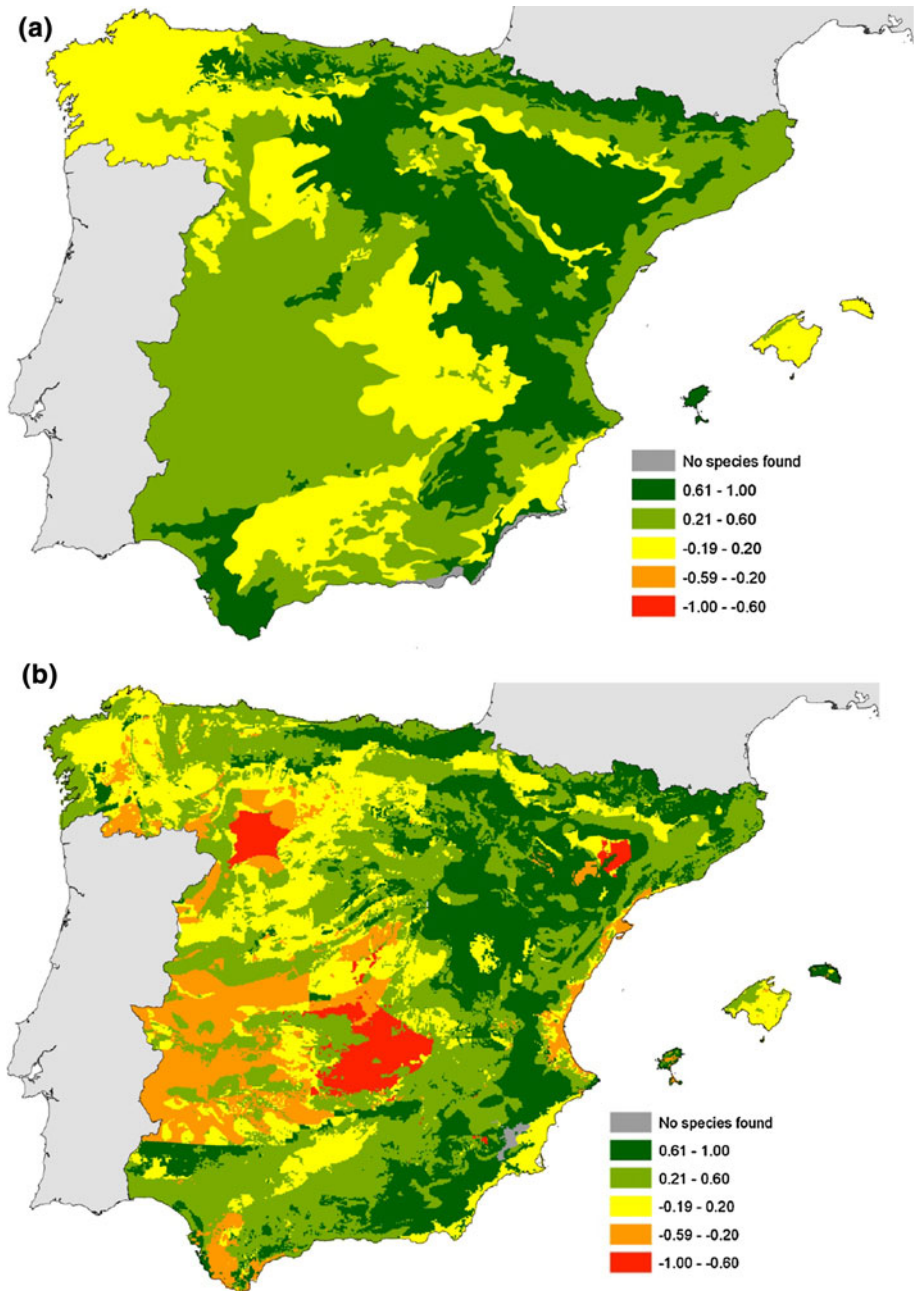


Fig. 2 Absent species ratio (AS) for **a** landscapes types (AS_l) and **b** biogeoclimatic classes (AS_b)

biogeoclimatic class. In contrast, *P. uncinata* is the most restrictedly distributed species (4 landscapes and 9 biogeoclimatic classes), being present in all of its potential range.

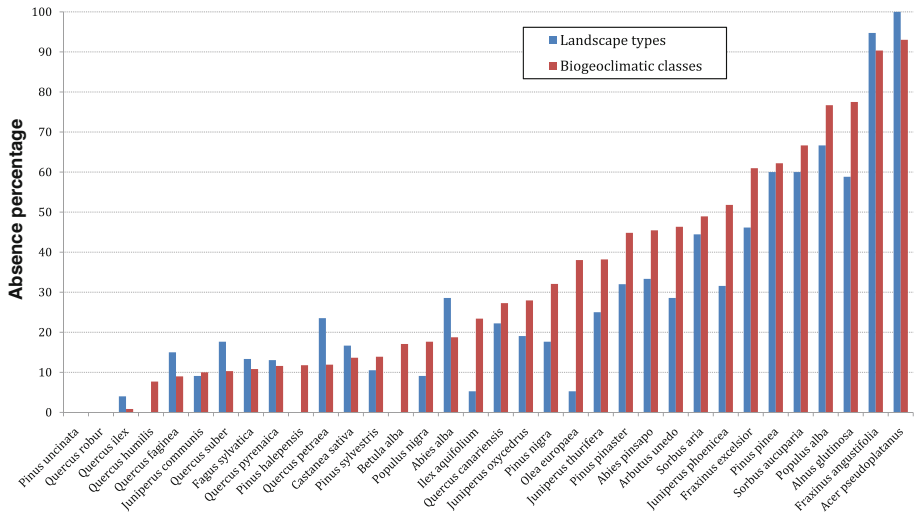


Fig. 3 Absence percentages of the species in relation with landscape types and biogeoclimatic classes

Discussion

Species distribution and richness

We present a method to estimate species pools at different scales (biogeoclimatic classes and forest landscape types) based on available information derived from National Inventories, autochthonous species distribution maps, and maximum entropy niche modeling methods. The MaxEnt prediction method is well suited for 85 % (34 out of 40) of the most important forest tree species in restoration and conservation programs in Spain (Jimenez et al. 2009). The species that fail to converge are those with distribution limitations that are clearly non-climatic.

The highest values of local tree species richness are found in mountainous areas of northern Spain with Atlantic climate and in zones in transition to a Mediterranean climate. These results agree with previous studies on woody species richness (Vetaas and Ferrer-Castán 2008) or vascular plants richness (Lobo et al. 2001).

It is interesting to notice that there is an important group of forest tree species that are far from their potential climatic niche, as is indicated by their Absence percentage. In general, the Absence percentage is weakly related to the analyzed life history-traits of the species, but it is connected with the land use of the area (i.e. RLUC- Ratio of Land use change). Moreover, different studies have shown the importance of soil characteristics on the potential distribution of species at the regional level (e.g. Regato et al. 1995 for *Pinus nigra*, Rubio et al. 2002 for *Castanea sativa*, Sánchez-Palomares et al. 2004 for *F. sylvatica*). This study, however, does not include soil variables, due to lack of data at the scale of the study that could explain the reduced current vs. potential distribution of some species. Soil restrictions are determinant in the distribution of some forest tree species (e.g. Oliet et al. 2009). For example, *P. pinaster* and *Quercus pyrenaica* are absent in calcareous zones, *P. pinea* is mainly extended in coastal or inland sands or very poor soils, and *J. thurifera* is a dominant species in continental calcareous highlands, due to a combination of extreme climatic conditions and pauperized soils.

Species richness at different scales: Plots, Biogeoclimatic classes and Landscape types

The Absent species ratio (AS) decreases from east to west in the north of the Peninsula, from high to low altitudes in inner ranges and plateaus, reaching a minimum in river valleys and on coastal zones. Such marked trend is related to the concentration of extensive and intensive agricultural land uses in these zones, but also related to fire disturbance and the traditional use of forest resources (Maetzke 2011). Traditional uses promoted the regeneration of the main species in each stand but not of the secondary ones (Scarascia-Mugnozza et al. 2000), as non-productive species were systematically eradicated or avoided altogether. Average observed species richness at the plot scale reaches 1.43 ± 3.80 species (Table 3). This value of species richness shows a trend close to monospecificity at the stand level, and suggests a pattern of a patchy landscape composed of stands in which tree species richness at the local level has not been promoted.

When assessing observed versus predicted tree species richness, the inclusion of ecological criteria for defining aggregation scale in relation to initial data plot has several consequences. Firstly, there is an increase in the average number of observed species richness (from 1.43 ± 1.45 to 6.03 ± 3.79 for biogeoclimatic classes and 8.02 ± 4.37 for landscape types) in accordance with the increased average area. Secondly, the increment in the predicted species richness is not as great as the observed richness (from 7.4 ± 3.8 to 9.46 ± 4.85 for biogeoclimatic classes and 11.04 ± 5.36 for landscape types) because there is a reduction of the figures of species' potentiality in accordance with the biogeoclimatic or forest typology restriction applied. In conclusion, including ecological criteria for defining aggregation scale brings a realistic approach to the number of species that are absent at each scale as a prerequisite to define a species pool for reforestation and restoration activities. This pool should be downscaled taking into account, among other factors, the ecological characteristics at the local level and the suitability and availability of forest reproductive materials, linked to the origin and other characteristics of basic materials (Young et al. 2005).

Table 3 Mean values of species richness at three geographical scales

	Grid UTM $1 \times 1 \text{ km}^2$	Biogeoclimatic classes	Landscape types
Total number	498,146	215	52
Mean area (km^2)	1.0	2,341.8	9,043.0
Predicted species richness			
Average	7.40	9.46	11.04
Standard deviation	3.80	4.85	5.36
Maximum–minimum	(25–0)	(26–0)	(25–1)
Observed species richness			
Average	1.43	6.03	8.02
Standard deviation	1.45	3.79	4.37
Maximum–minimum	(11–0)	(21–0)	(20–1)
Absent species			
Average	6.03	3.43	3.02
Standard deviation	3.22	2.23	2.11
Maximum–minimum	(23–0)	(10–0)	(10–0)

Application to restoration and conservation programs

Detection of potential species pool would assist in restoration of degraded landscapes by providing forest species propagules of the site-specific varieties best adapted to future climatic conditions, even though they may be different from the present forest-plant community (de Dios et al. 2007).

For restoration programs, we have identified a suitably large species pool for each region and at different scales. Deciding the relative importance of a species within its pool for restoration is key in planning restoration or forestation programs (Zedler 2005).

There is a general tendency to dominance of a reduced number of species (mainly *Pinus* and *Quercus*) across extensive zones of territory. The non-dominant species are those with the lowest observed frequency across the territory. In consequence, it would be convenient to increase species diversity in restoration programs, especially in order to attempt to build more resilient systems for the future (Harris et al. 2006).

Conclusions

The different approaches to land aggregation (biogeoclimatic classes or forest landscapes) affect the pool of absent species estimates. Therefore, when type or scale of aggregation is not considered, the species pool available for restoration also differs. According to the results of this study, a biogeoclimatic classification seems more suitable than the potential forest landscapes types, because it includes a wider variety of biogeoclimatic conditions that are closer to niche modeling.

The Absence percentage of species can help to understand the historical absence of tree species, due not only to human land uses, but also to colonization or dispersion deficiencies. In general, non-dominant species, not subjected to forest management, and zonal species usually show a higher Absence percentage from the suitable landscapes or biogeoclimatic classes than those species dominant at stand level and subjected to forest management.

Future restoration programs must give special consideration to those species that are poorly distributed in the present but carry great potential for increased diversity and stability for forest systems, not only in the present climatic conditions, but also in future climate scenarios.

Acknowledgments We thank Helios Sáinz Ollero and Rut Sánchez de Dios for kindly providing the digital shape file of the Spanish Forest Landscapes and Ramón Elena-Rosselló for providing the digital shape file of the CLATERES Territorial Classes. We also thank MARM for providing the data of the Third Spanish Forest Inventory. This work was supported by the Collaborative Project on 'Conservation of Forest Genetic Resources' between the Spanish Ministry of Environment and INIA (AEG06-054), and Project RTA2010-00120-C02-02. Thanks are extended to P.C. Grant, scientific editor, for the revision of the language.

References

- Alía R, García del Barrio JM, Iglesias S, Mancha JA, De Miguel J, Nicolás J, Pérez F, Sánchez de Ron D (2009) Regiones de Procedencia de Especies Forestales en España. O.A. Parques Nacionales. MARM, Madrid
- Austin MP, Pausas JG, Nicholls O (1996) Patterns of tree species richness in relation to environment in southeastern New South Wales. *Aust J Ecol* 21:154–164

- Blach-Overgaard A, Svenning JC, Dransfield J, Greve M, Balslev H (2010) Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints. *Ecography* 33:380–391
- Bolle H-J (ed) (2003) Mediterranean climate: variability and trends. Regional climate series. Springer, Berlin
- Brown KA, Spector S, Wu W (2008) Multi-scale analysis of species introductions: combining landscape and demographic models to improve management decisions about non-native species. *J Appl Ecol* 45:1639–1648
- Brudvig LA, Mabry CM (2008) Trait-based filtering of the regional species pool to guide understory plant reintroductions in Midwestern oak savannas, USA. *Restor Ecol* 16:290–304
- Bunce RGH, Barr J, Clarke RT, Howard C, Lan AMJ (1996) ITE Merlewood land classification of Great Britain. *J Biogeogr* 23:625–634
- Bunce RGH, Carey PD, Elena-Rosselló R, Orr J, Watkins J, Fuller R (2002) A comparison of different biogeographical classifications of Europe, Great Britain and Spain. *J Environ Manag* 65:121–134
- CE (1999) Directive 1999/105/CE on marketing of forest reproductive material in E. Union. Official Journal of the European Community
- Coudun C, Gegout J-C, Pledallu Ch, Rameau J-C (2006) Soil nutritional factors improve models of plant species distribution: an illustration with *Acer campestre* (L.) in France. *J Biogeogr* 33:1750–1756
- de Dios VR, Fischer C, Colinas C (2007) Climate change effects on Mediterranean forests and preventive measures. *New For* 33(1):29–40
- Elena-Rosselló R (1997) Clasificación Biogeoclimática de España Peninsular y Balear. Ministerio de Agricultura, Pesca y Alimentación. Madrid
- Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettman F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams JS, Wisz MS, Zimmermann ME (2006) Novel methods improve prediction of species distributions from occurrence data. *Ecography* 29:129–151
- Enright NJ, Miller BP, Crawford A (1994) Environmental correlates of vegetation patterns and species richness in the northern Grampians, Victoria. *Aust J Ecol* 19:159–168
- Ferrer-Castán D, Vetaas OR (2005) Pteridophyte richness, climate and topography in the Iberian Peninsula: comparing spatial and nonspatial models of richness patterns. *Global Ecol Biogeogr* 14:155–165
- Gonzalo J (2010) Diagnóstico fitoclimático de la España Peninsular. Hacia un modelo de clasificación funcional de la vegetación y de los ecosistemas peninsulares españoles. *Naturaleza y Parques Nacionales. Serie Técnica. Organismo Autónomo Parques Nacionales. MMRM, Madrid*
- Guisan A, Thuiller W (2005) Predicting species distribution; offering more than simple habitat models. *Ecol Lett* 8:993–1009
- Guisan A, Zimmermann NE, Elith J, Phillips SJ, Peterson AT (2007) What matters for predicting the occurrences of trees: techniques, data, or species characteristics? *Ecol Monogr* 77:615–630
- Hanspach J, Kühn I, Pompe S, Klotz S (2010) Predictive performance of species distribution models depends on species traits. *Perspect Plant Ecol* 12:219–225
- Harris JA, Hobbs RJ, Higgs E, Aronson J (2006) Ecological restoration and global climate change. *Restor Ecol* 14:170–176
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2004). The WorldClim interpolated global terrestrial climate surfaces. Available at <http://biogeog.berkeley.edu/>
- Holmes PM, Richardson DC (1999) Protocols for restoration based on recruitment dynamics, community structure, and ecosystem function: perspectives from South African fynbos. *Restor Ecol* 7:215–230
- Jaynes ET (1957) Information theory and statistical mechanics. *Phys Rev* 106:620–630
- Jimenez P, Díaz-Fernández P, Iglesias S, Prada A, García del Barrio JM, Alba N, Alía R (2009) National strategy for the conservation and sustainable use of forest genetic resources: a framework for coordinating Central and Autonomous Regional Government activities in Spain. *Inv Agrar: Sist y Rec For* 18:13–19
- Jones TA, Monaco TA (2009) A role for assisted evolution in designing native plant materials for domesticated landscapes. *Front Ecol Environ* 7:541–547
- Kadoya T, Suda S, Nishihiro J, Washitani I (2008) Procedure for predicting the trajectory of species recovery based on the nested species pool information: Dragonflies in a wetland restoration site as a case study. *Restor Ecol* 16:397–406
- Levich AP (2000) Variational modelling theorems and algocoenoses functioning principles. *Ecol Model* 131:207–227
- Lobo JM, Castro I, Moreno JC (2001) Spatial and environmental determinants of vascular plant species richness distribution in the Iberian Peninsula and Balearic Islands. *Biol J Linn Soc* 73:233–253

- Maetzke F (2011) Systematic silviculture and Mediterranean forest complexity: the need for a new paradigm in forestry. *Ital J For Mt Environ* 66:229–232
- MCPFE (2007) Pan-European Recommendations for Afforestation and Reforestation in the context of the UNFCCC. Ministerial Conference on the Protection of Forests in Europe, Warsaw
- Médail F, Quézel P (1999) Biodiversity hotspots in the mediterranean basin: setting global conservation priorities. *Conserv Biol* 13:1510–1513
- Miller AJ, Knouft JH (2006) GIS-based characterization of the geographic distributions of wild and cultivated populations of the Mesoamerican fruit tree *Spondias purpurea* (Anacardiaceae). *Am J Bot* 93:1757–1767
- Ministerio de Medio Ambiente -MMA- (2002). Mapa forestal de España escala 1:50.000 (MFE50)
- Ohmann JL, Spies TA (1998) Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecol Monogr* 68:152–182
- Oliet J, Planelles R, Artero F, Valverde R, Jacobs D, Segura M (2009) Field performance of *Pinus halepensis* planted in Mediterranean arid conditions: relative influence of seedling morphology and mineral nutrition. *New Forest* 37(3):313–331
- Ortega M, Metzger MJ, Bunce RGH, Wrbka T, Allard A, Jongman RHG, Rob HG, Elena-Rosselló R (2012) The potential for integration of environmental data from regional stratifications into a European monitoring framework. *J Environ Plann Man* 55:39–57
- Phillips SJ, Dudik M, Schapired RE (2004) A maximum entropy approach to species distribution modeling. In: 21st international conference on machine learning, Banff, Canada
- Phillips SJ, Anderson RP, Schapired RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Mod* 190:231–259
- Pueyo S (2006) Diversity: between neutrality and structure. *Oikos* 112:392–405
- Pueyo S, He F, Zillio T (2007) The maximum entropy formalism and the idiosyncratic theory of biodiversity. *Ecol Lett* 10:1017–1028
- Regato P, Gamisans J, Gruber M (1995) A syntaxonomical study of *Pinus nigra* subsp. *salzmannii* forests in the Iberian Peninsula. *Phytocoenología* 25:561–578
- Rodríguez-Sánchez F, Hampe A, Jordano P, Arroyo J (2010) Past tree range dynamics in the Iberian Peninsula inferred through phylogeography and palaeodistribution modelling: a review. *Rev Palaeobot Palyno* 162:507–521
- Rubio A, Sánchez Palomares O, Gómez V, Graña D, Elena-Rosselló R, Blanco A (2002) Autoecología de los castaños de Castilla (España). *Invest Agr: Sist Recur For* 11(2):373–393
- Ruiz de la Torre J (2006) Flora Mayor. O. A. Parques Nacionales. Ministerio de Medio Ambiente, Madrid 1757 pp
- Sainz-Ollero H, Sánchez de Dios R, García-Cervigón A (2010) La cartografía sintética de los paisajes vegetales españoles: una asignatura pendiente en Geobotánica. *Ecología* 23:249–272
- Sánchez-Palomares O, Rubio A, Blanco A (2004) Definición y cartografía de las áreas potenciales fisiográfico-climáticas de hayedo en España. *Invest Agrar, Sist Recur For Fuera de serie*, pp 13–62
- Scarascia-Mugnozza G, Oswald H, Piussi P, Radoglou K (2000) Forest on the Mediterranean region: gaps in knowledge and research needs. *For Ecol Manag* 132:97–109
- Scott CE, Alofs KM, Edwards BA (2011) Putting dark diversity in the spotlight. *TREE* 26:263–264
- SER (2004) Society for Ecological Restoration International Science & Policy Working Group. The SER International Primer on Ecological Restoration. www.ser.org & Tucson: Society for Ecological Restoration International
- Shiple B, Vile D, Garnier E (2006) From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science* 314:812–814
- Soria-Auza RW, Kessler M, Bach K, Barajas-Barbosa PM, Lehnert M, Herzog SK, Bohner J (2010) Impact of the quality of climate models for modelling species occurrences in countries with poor climatic documentation: a case study from Bolivia. *Ecol Model* 221:1221–1229
- Stockwell DRB, Peterson AT (2002) Effects of sample size on accuracy of species distribution models. *Ecol Model* 148:1–13
- Svenning J-C, Skov F (2007) Ice age legacies in the geographical distribution of tree richness in Europe. *Global Ecol Biogeogr* 16:234–245
- Thuiller W, Lavorel S, Sykes MT, Araujo MB (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Divers Distrib* 12:49–60
- Vallejo VR (2010) Problems and perspectives of dryland restoration. In: Bautista S, Aronson J, Vallejo VR (eds) Land restoration to combat desertification. Innovative approaches, quality control and project evaluation. Fundación CEAM, Paterna, pp 13–22
- Vetaas OR, Ferrer-Castán D (2008) Patterns of woody plant species richness in the Iberian Peninsula: environmental range and spatial scale. *J. Biogeography* 35:1863–1878

-
- Villanueva J (2004) Tercer Inventario Forestal Nacional (1997–2007). Comunidad de Madrid. Ministerio de Medio Ambiente, Madrid
- Williams CB (1964) Patterns in the balance of nature. Academic Press, London
- Williams JN, Seo CW, Thorne J, Nelson JK, Erwin S, O'Brien JM, Schwartz MW (2009) Using species distribution models to predict new occurrences for rare plants. *Divers Distrib* 15:565–576
- WWF (2009) Bosques españoles. Los bosques que nos quedan propuesta de WWF para su restauración. WWF España. Ministerio de Medio Ambiente Rural y Marino, Madrid
- Young TP, Petersen DA, Clary JJ (2005) The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecol Lett* 8:662–673
- Zedler J (2005) Ecological restoration: guidance from theory. *San Francisco Estuary and Watershed Science* 3(2). 31 pp
- Zobel M, van der Maarel E, Dupré C (1998) Species pool: the concept, its determination and significance for community restoration. *Appl Veg Sci* 1:55–66