

A novel application of the ecological field theory to the definition of physiographic and climatic potential areas of forest species

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Abstract A new approach to the definition of physiographic and climatic potential areas for forest species, based on the ecological field theory, is outlined in this paper. The proposed formulation is tested on the Spanish juniper (*Juniperus thurifera* L.), using data from 883 permanent and temporary plots throughout its distribution area in the Spanish autonomous region of Castilla y León. The suitability of the territory for the species is assessed by previously studying its habitat, which in turn is analyzed through physiographic and climatic parameters. This new method is rooted in an additive index that depends on the Mahalanobis distance in the parametric space that evaluates the ecological resemblance between the studied site and each of the points defining the parametric habitat. Thereby the ecological potential of any site within the territory can be established, integrated in a geographical information systems and accordingly charted. The results are compared with those obtained with the methodology traditionally used by Spanish foresters (factorial index), showing that the overall potential area is similar in size but quite different in its distribution.

Keywords Ecological potential · Mahalanobis' distance · *Juniperus thurifera* · Autecology

Introduction

Current European Union agrarian policy boosts the abandonment of the least productive agricultural lands in favor of productive (to obtain wood and other resources) or protective reforestations (to contribute to the fight against desertification, the conservation of biodiversity, and others) (Rubio and Sánchez Palomares 2006). In order to plan this task and in addition to other aspects, forest managers need to know as accurately as possible of which species are suitable for use in each site (Felicísimo et al. 2002; Guisan and Thuiller 2005; Serrada 2005; Edenius and Mikusiński 2006). Therefore, it is essential to envisage, for each forest species, its capacity for living at each site where it is absent, that is, to be able to predict its potential distribution area.

The study of a species' autecology is the previous and necessary step in order to work out predictive models of the potential distribution area. This can be tackled from many conceptual and methodological standpoints. Nevertheless, nowadays one aspect common to all of them is the use of multivariate statistical techniques and geographical information systems (GIS) (Guisan and Zimmermann 2000). The latter permit autecological studies to be undertaken on a regional scale with great agility and accuracy when reliable digital elevation models (DEMs) are available.

During the last 40 years of forest autecological research in Spain, a subject-specific methodology based on the environmental envelope techniques has been tailored and improved, although the ecological parameters have always been the raw material for each species' potential distribution

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area. Thus, the methodological foundation is based on the calculation of those parameters in the whole territory where the species' potentiality is to be estimated (Sánchez Palomares 2001). Both physiographic and climatic parameters can be drawn almost directly from a DEM, as models for predicting climatic variables depending on geographical position and altitude (ALT) are available (Sánchez Palomares et al. 1999); unfortunately, this does not occur with edaphic parameters. The current available information for soil properties is either too coarse, or qualitative. This prevents us from calculating in continuum edaphic and edaphic-climatic parameters and, subsequently, edaphic and edaphic-climatic potential areas. Moreover, the models developed for the Spanish forest autecological studies can be included in those that have been referred to as profile techniques, that is, those that use only presence locality records (Robertson et al. 2003).

Another essential issue in the process of estimating the suitability of a site for a forest species is the mathematical method employed in the calculation of the numeric potentiality indicator. Even if many of the approaches in the literature are considered irreproachable from a conceptual and scientific point of view (Guisan and Zimmermann 2000; Anderson et al. 2003; Benito Garzón et al. 2006), they are hardly applicable in practice. Therefore, they are not very popular among forest practitioners (Rubio and Sánchez Palomares 2006). For this reason Gandullo and Sánchez Palomares (1994) proposed a very conservative method that was subsequently modified by Sánchez Palomares et al. (2004) through employing a factorial potentiality index (FPI), as explained below. In this work, we propose a novel potentiality index founded on the application of the Mahalanobis' distance to the ecological field theory (EFT).

The so-called EFT was outlined by Wu et al. (1985) with the aim of describing spatial interference among plants and in turn modeling the competition for water, light, nutrients and other resources. The concept behind EFT was based on the common field theory of physics and was developed by Walker et al. (1989), who established its key components: the influence domain of individuals, the field intensity between domains, the influence surface and the intensity of interactions.

The application of this methodology has been very fruitful. Thus, it has been employed to demonstrate theoretically the self-thinning law in crowded, even-aged stands (Li et al. 2000), establishing a general rule for self-thinning that satisfactorily explains the different exponents of the function empirically found. Fernández et al. (2002) adapted the EFT for its use in the quantification of the border effect in fragmented ecosystems by the integration of the infinitesimal effect created by each border point. This continuous approach also provided adequate results when

developing distance-dependent growth models for *Pinus sylvestris* L. and *Picea abies* (L.) Karst. stands (Miina and Pukkala 2002). Continuing in the silvicultural field, Sipilä et al. (2006) employed the EFT to model height distribution of Scots pine saplings depending on the influence of retained trees and the distance to the stand edge. From a synecological standpoint, the EFT has also been useful in contributing to the debate on the Gleasonian and Clementsonian conception of plant communities (Feagin et al. 2005). Finally, EFT has even been exported to the animal kingdom for modeling extinctions, prey–predator interactions, etc. (Nakagiri and Tainaka 2004).

All these examples of the application of EFT are performed in the real world, which is a Euclidean space. Nevertheless, the concept of interaction at a distance can be used in other frameworks. In this paper, we aim to outline a methodology for the EFT to be tailored to a multidimensional space with non-orthogonal axes in order to develop predictive habitat distribution models. Specifically, our goals have been (1) to modify the habitat definition methodology used by classical autecology studies in Spain in order to consider underlying compensation effects among parameters and (2) to specify a new suitability index defined in the multivariate parametric space and based on the Mahalanobis' distance.

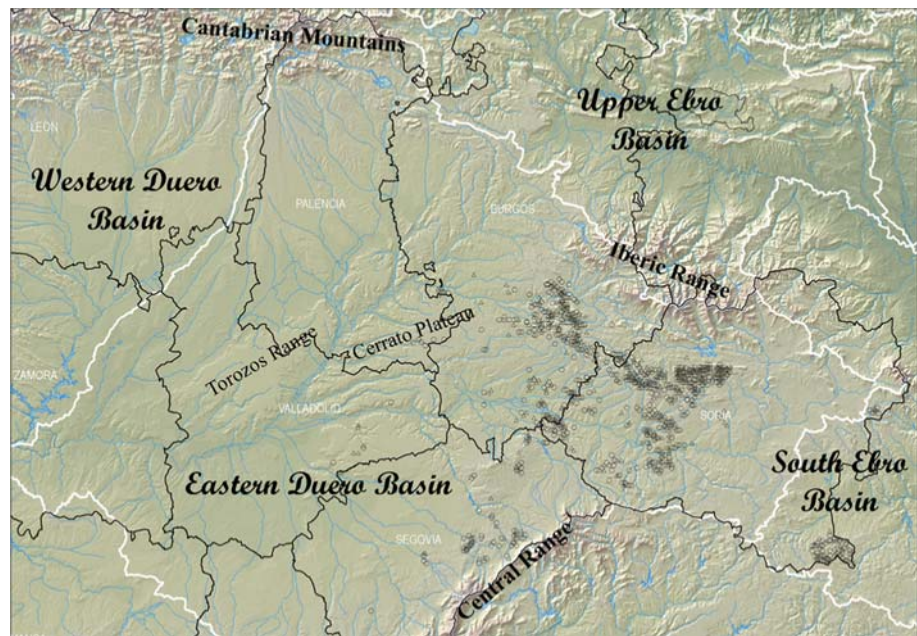
Methods

Data

The methodology presented in this work was tested on the Spanish juniper (*Juniperus thurifera* L.) distribution in the Spanish region of Castilla y León, (central northern Spain), according to the data provided by the Third National Forest Inventory (3NFI). Thus, 813 plots with *J. thurifera* as the first, second or third species with the highest basal area values were selected. An ancillary set of 70 temporary plots were added to complete the current distribution area of the species in the autonomous region (Fig. 1).

The following ecological parameters were calculated for each selected plot, according to the criteria used in previous autecological parametric studies developed in Spain (Gandullo and Sánchez Palomares 1994; Rubio et al. 2002). The physiographic parameters are ALT measured in meters, slope (SLP) in percentage, insolation index (INS) (Gandullo 1974) and thermic-topographic index (TTP) (Gandullo 1997), both as a function of SLP and aspect. The models for climatic estimation developed by Sánchez Palomares et al. (1999), which are functions of ALT, geographical position (coordinates X and Y of UTM in the zone 30) and the hydrographical basin where each site is located were used to calculate 15 climatic parameters:

Fig. 1 Study area with the 883 plots used in the analysis (circles, *J. thurifera*-dominated plots; triangles, *J. thurifera*-non-dominated plots). Hydrographical basins are delimited with white lines



mean annual rainfall (MAR), mean spring rainfall (SPR), mean summer rainfall (SMR), mean autumn rainfall (ATR) and mean winter rainfall (WTR) measured in millimeters; mean annual temperature (MAT), mean of the highest temperature of the hottest month (HHT) and mean of the lowest temperature of the coldest month (LCT), measured in degrees centigrade; sum of the 12 monthly potential evapotranspirations (PET), annual moisture surplus (SUP), annual moisture deficit (DEF), measured in millimeters, annual hydric index (HI) (Thorntwaite and Mather 1957); length of drought duration measured in months (LDR) and intensity of drought (IDR) in percentage (Walter and Lieth 1960); and finally the Vernet index (VERN) (Vernet and Vernet 1966).

Habitat characterization

Using the values of the 19 parameters listed above the physiographic and climatic habitat has been characterized following the methodology of Gandullo et al. (1974), also utilized in other studies about potential area models in Spain (Sánchez Palomares et al. 2004; Rubio and Sánchez Palomares 2006), with the modifications introduced by Alonso Ponce (2008). Thus, in the former works, the lower and upper limiting values (LL and UL respectively) are established as the absolute minimum and maximum for each parameter. Furthermore, the lower and upper threshold values (LT and UT) are located as the minimum and maximum values for each parameter excluding the 10% of observations where the parameter reaches its lowest value and the 10% where it reaches the highest value. Nevertheless, Alonso Ponce (2008) introduced a new concept, the

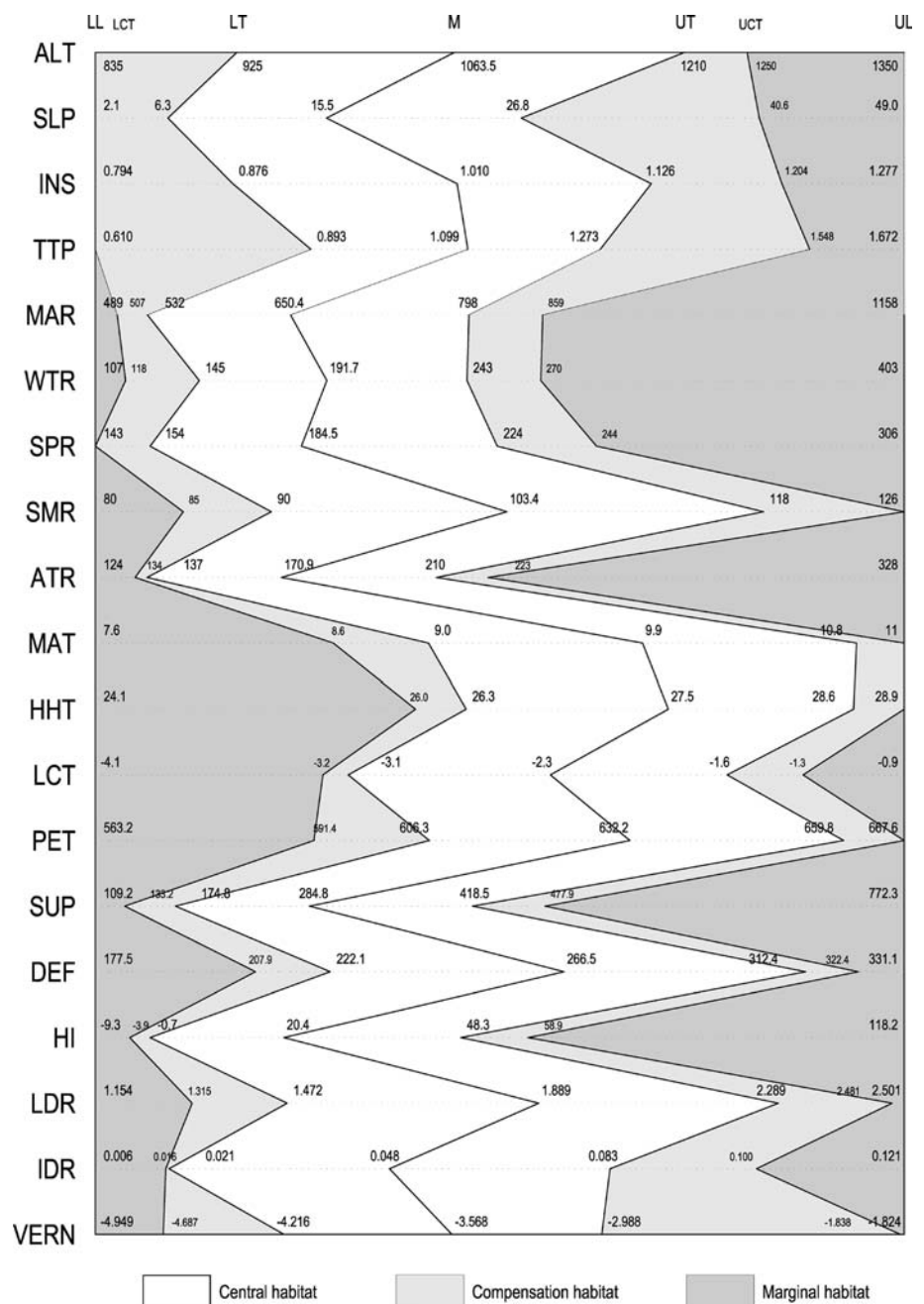
lower and upper compensation thresholds (LCT and UCT), which are defined as the lowest and highest values of each parameter in the subset of the 80% nearest observations to the center of gravity (means vector, M), as calculated in the 19-dimensional parametric space (P). High correlations are usually found among ecological parameters; therefore, the Mahalanobis' distance is advisable for the assessment of ecological resemblance among observations (Legendre and Legendre 1998). Then, we define a central band (interval between LT and UT), two compensation bands (intervals between LCT and LT and between UT and UCT), and two marginal bands (intervals between LL and LCT and between UCT and UL). The diagram in Fig. 2 shows, for each parameter, the physiographic and climatic habitat of Spanish juniper in the Castilla y León region. From a physiographic and climatic point of view, a location whose parameter values all fall within the central band can be considered as highly suitable for the species. If all or some of the parameters fall within the compensation bands the studied site must be seen as a marginal place where compensation among ecological factors relieves such marginality, while if they fall inside the marginal bands, such compensation is not expected and consequently its suitability lessens dramatically.

Habitat suitability indexes

Additive index

The index proposed here bases its formulation on the EFT, although the calculation space is not the real three-dimensional Euclidean space but the multidimensional

Fig. 2 Diagram of the physiographic and climatic habitats of *J. thurifera* in the Spanish region of Castilla y León



non-Euclidean parametric space. The EFT considers that any plant is surrounded by a circular influence field whose size (domain) depends on the size of the plant, and whose intensity decreases with distance (Walker et al. 1989). Our approach proposes that each observation (plot defining the habitat) behaves in the parametric space as each plant does in the real one. Thus, a region of the parametric space crowded with observations indicates high potentiality, whereas those remote areas far from any observation show low suitability for the species.

To quantify the ecological potential that the whole set of observations creates on each point of *P*, a

distance-dependent function is to be used (potential function), which must comply with the following: (1) it must allow the final index to be additive; (2) it must be monotonically decreasing with distance; and (3) paralleling a probability function, it must vary between 0 and 1. The second requirement can be directly drawn from the definition of the EFT, while the third is assumed to permit the comparison between analyses carried out in different territories, unlike number of observations. The first one will be justified below, when the final index is defined.

Any bell-shaped function complies with the two first conditions, and the third one is easily achieved by

eliminating any factor of the number e . Hence, a valid function for our goals is:

$$f(d) = e^{-(d/b)^2} \tag{1}$$

where d is the Mahalanobis’ distance between an observation and the point of P where potentiality is to be calculated and b is an arbitrary variable (we used $b = 5$), so-called penetration, which allows different values of $f(d)$ to be assigned to equal distances depending on the parametric region of the habitat where the observation is located, as shown below.

Thus, let D_C be the region of P defined by the subset of the 80% nearest observations to the center of gravity (“compensation central habitat”). Any observation located inside D_C (that is, at a distance d_i to center of gravity shorter than d_C , border of D_C) will create a potential at a distance d equals the value of the Eq. 1. Nevertheless, in order to reduce the penetration of those observations localized outside the borders of D_C , which are expected to be less suitable for the species, the potential function is redefined as follows:

$$f_M(d) = e^{-(db_M)^2} \tag{2}$$

where b_M is:

$$b_M = \frac{b}{1 + (d_i - d_C)} \tag{3}$$

Thus, when calculating the potential created by an observation situated just on the border of the compensation central habitat $b_M = b$, while if it is outside D_C (i.e., $d_i > d_C$) then $b_M < b$ and therefore its penetration and consequently the potential created around it will be lower.

Finally, the potentiality at any point of P will be the sum (hence its additive feature) of the potentials created by all the observations defining the habitat. Hence, the additive potentiality index (API) is:

$$API = \frac{1}{C + M} \left[\sum_{i=1}^C f_C(d_i) + \sum_{i=1}^M f_M(d_i) \right] \tag{4}$$

where C is the number of observations inside D_C and M the number of observations outside D_C . Dividing by the overall number of observations (hence API is the mean of the potential at the studied point) makes the index vary between 0 and 1, as was desired.

In order to elucidate the deep repercussion that the strong correlations existing between parameters have on API, and therefore the justification of the use of the Mahalanobis’ distance, Fig. 3 shows the calculation of API in the two-dimensional parametric space defined by two highly correlated variables, MAR and MAT ($\rho = -0.97$; $P < 0.001$). Figure 3a shows the result using the Euclidean distance and Fig. 3b the Mahalanobis’ distance. It is striking that the potentiality function narrows in the latter, where points of the parametric plane seemingly near (due to our intuitive Euclidean notion of the space) to the cloud of observations receive very low potentiality values, for they do not fit the sharp trend reflected in the correlation coefficient. In Fig. 4 (a, Euclidean distance; b, Mahalanobis’ distance) the same calculations have been made on a manipulated data set in such a way that the correlation coefficient sinks to 0.27 ($P > 0.05$). In this case, the use of any of the two distances brings about very similar potential functions.

Factorial index

Sánchez Palomares et al. (2004) proposed a factorial index, based on the initial formulation of Gandullo and Sánchez Palomares (1994) to determine the potential areas for forest species, which has been used by Spanish foresters (Cisneros 2004; Sarmiento 2005; Rubio and Sánchez Palomares 2006) so far. Just like the additive index, the definition of a species’ habitat is the basis for appraising

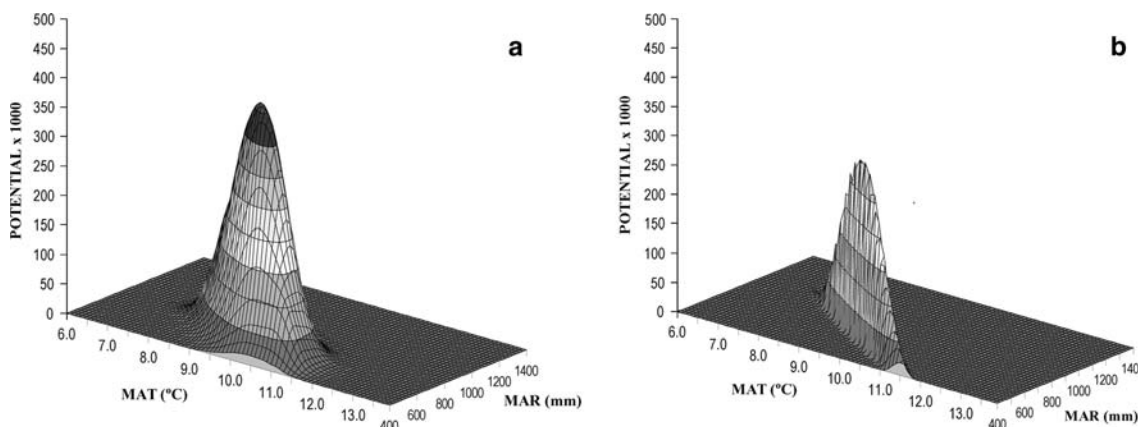


Fig. 3 Plot of API calculated in the two-dimensional parametric space of highly correlated axes (MAR and MAT), employing the Euclidean distance (a) and the Mahalanobis’ distance (b)

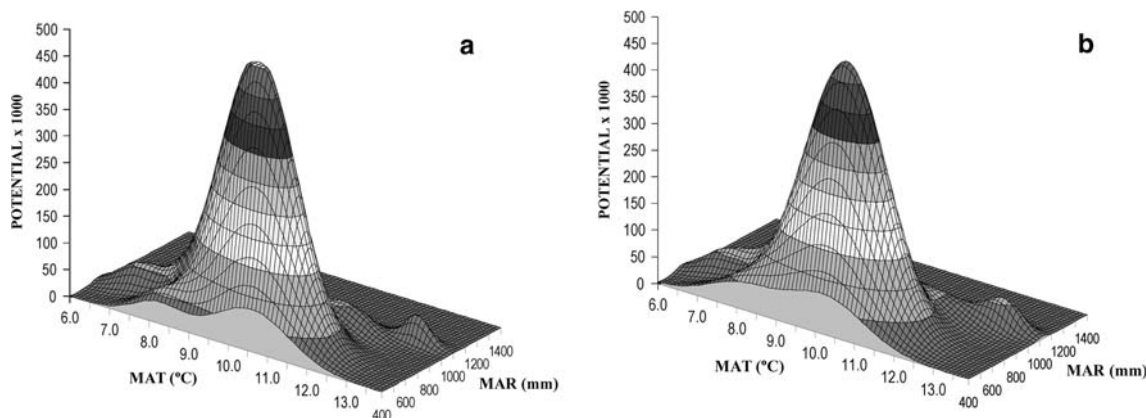


Fig. 4 Plot of API calculated in the two-dimensional parametric space of poorly correlated axes (MAR and MAT, manipulated data set), employing the Euclidean distance (a) and the Mahalanobis’ distance (b)

the suitability of a site for a particular taxon. Nevertheless, in the case of FPI no compensation thresholds are specified, hence only three bands are taken into account: two marginal (upper and lower) and one central. The contribution of each parameter to the greater or lesser suitability of a given site will depend on the band where the parameter value falls. Although the formulation of this index has already been reported in international forest literature (Rubio and Sánchez Palomares 2006), here we will briefly abridge its basic features for a better understanding.

Thus, let i be a parameter whose value in the studied location is x_i . As explained above, i has its LL_i , LT_i , M_i , UT_i and UL_i . The suitability indicator p_i is defined as follows:

- If $x_i = M_i \Rightarrow p_i = 1$
- If $x_i \in [LT_i, UT_i] \Rightarrow p_i = 1 - \frac{|M_i - x_i|}{UT_i - LT_i}$
- If $x_i \in [LL_i, LT_i] \Rightarrow p_i = \frac{(UT_i - M_i) \cdot (x_i - LL_i)}{(UT_i - LT_i) \cdot (LT_i - LL_i)}$
- If $x_i \in [UT_i, UL_i] \Rightarrow p_i = \frac{(M_i - LT_i) \cdot (UL_i - x_i)}{(UT_i - LT_i) \cdot (UL_i - UT_i)}$

- If $x_i \notin [LL_i, UL_i] \Rightarrow p_i = 0$

Such a definition poses an indicator proportional to the distance between x_i and M_i while x_i belongs to the central habitat and that linearly diminishes from the value acquired at UT_i to 0 at UL_i , or the value acquired at LT_i to 0 at LL_i .

Finally, the FPI is defined as the product of every p_i obtained for each parameter:

$$FPI = \frac{1}{NP} \log \left(\prod_{i=1}^{NP} p_i 10^4 \right) \tag{5}$$

where NP is the number of parameters. The use of the log function and the 10^4 factor has the exclusive purpose of making FPI vary between 0 and 4.

Paralleling the two-dimensional example for API, Fig. 5a and b shows the potential functions generated with FPI using the same data (a, highly correlated; b, poorly correlated). Obvious differences can be noticed when comparing with API graphs, as FPI predicts high potentiality for regions of the parametric plane, whereas API prognosticates almost no suitability.

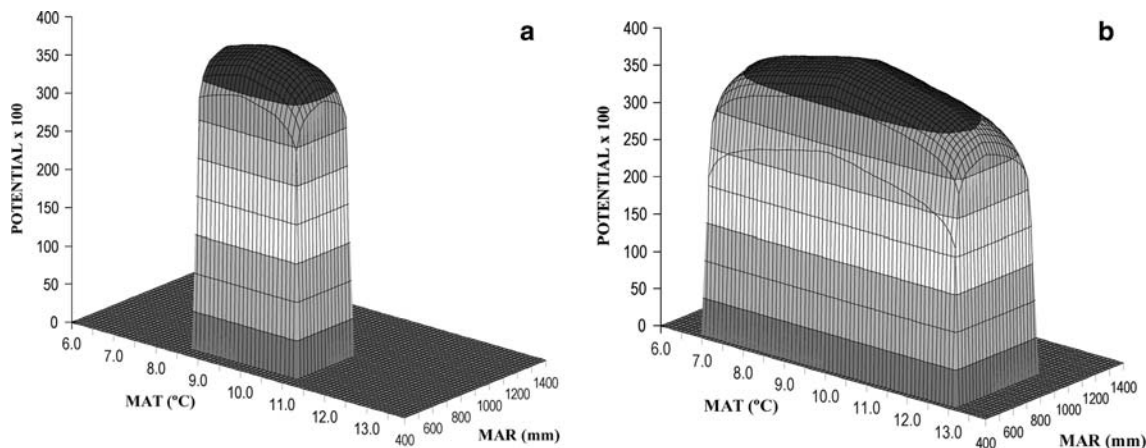


Fig. 5 Plot of FPI calculated in the two-dimensional parametric space of a highly correlated axes (MAR and MAT) and b poorly correlated axes (MAR and MAT, manipulated data set)

Table 1 Limits of potentiality classes for FPI (factorial potentiality index) and API (additive potentiality index)

Limits for FPI	Limits for API	Potentiality
$FPI \geq 3.85$	$0.25 \leq API < 1.00$	Optimum
$3.75 \leq FPI < 3.85$	$0.10 \leq API < 0.25$	High
$3.65 \geq FPI < 3.75$	$0.01 \leq API < 0.10$	Medium
$FPI < 3.65$	$0.0011 \leq API < 0.01$	Low

Calculations for both indexes have been developed with SAS/IML and results have been subsequently implemented into regional maps through Arc/Info 9.1.

Potentiality classes

Models generated with API and FPI make it possible to assign potentiality to each point of the territory of Castilla y León, and accordingly to generate suitability maps. For these maps to be clear enough and useful for forest managers, it is advisable to establish potentiality classes, depending on the extremes obtained for the indexes. Table 1 shows the limits of the four proposed classes, for both indexes, which roughly correspond with the quartiles of their distributions. The lower limit of class 4 of API stems from the value of potentiality which a site would have if it were situated exactly in the same point of the parametric space occupied by an observation (current site for the studied species), extremely isolated (in the parametric space) from the cloud of observations defining the habitat. Thus, the potential (1, as $f(0) = 1$) of that point should be exclusively created by that observation, and as the number of observations in our practical case is 883, then $1/883 = 0.0011$.

Model evaluation

Evaluation through current vegetation

To assess the validity of the habitat distribution models, data from the 3NFI will be used, as this kind of comprehensive and systematic inventory represents a highly valuable information source for autecological studies (Charnet 2001; Gégout 2001). The method, already utilized for other Spanish species (López Senespleda et al. 2006; Montero et al. 2006; Rubio and Sánchez Palomares 2006), consists of analyzing the occupation of the potentiality classes by the different tree species which form the current forest vegetation.

Evaluation through climax vegetation

A second assessment of the potentiality areas is carried out using the proposed phytosociological vegetation series

maps (Rivas-Martínez 1987) for the region, according to the synthesis developed by Vázquez et al. (2002). As in the case of the current vegetation, the phytosociological vegetation series map is overlaid with the potentiality maps.

Results

Physiographic and climatic potentiality models

The physiographic and climatic suitable areas for Spanish juniper in Castilla y León have been defined following the two indexes defined above, and have been mapped in Fig 6a (FPI) and b (API). In addition, in Table 2 the surface (in km²) occupied by each potentiality class (for both indexes) in each province is listed. Both indexes produce similar overall potentiality areas (about 30,000 km²), but their distribution through provinces and classes are rather different.

Thus, FPI predicts large low potentiality areas in the Cantabrian Mountains, while API predicts these areas as

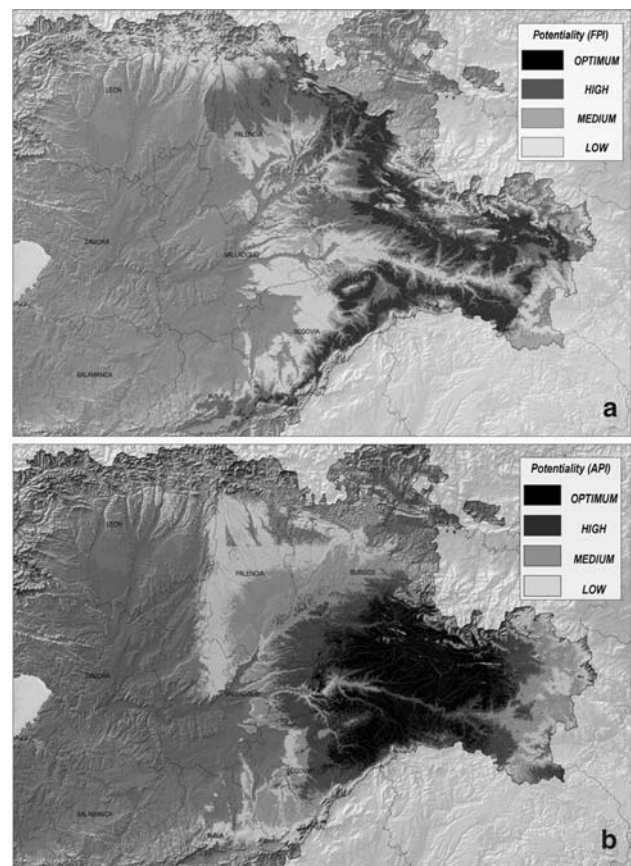


Fig. 6 **a** Physiographic and climatic potential areas of *J. thurifera* in the Spanish region of Castilla y León according to FPI. **b** Physiographic and climatic potential areas of *J. thurifera* in the Spanish region of Castilla y León according to API

Table 2 Area (km²) occupied by each physiographic and climatic potentiality class of *J. thurifera* in the region of Castilla y León, for both indexes (FPI, factorial potentiality index; API, additive potentiality index) and by provinces

Province	FPI					API				
	Optimum	High	Medium	Low	Total	Optimum	High	Medium	Low	Total
Ávila	63.5	658.2	203.5	113.8	1039.0	0.0	0.0	64.7	523.9	588.6
Burgos	2314.4	3112.3	1516.7	1299.3	8242.7	3004.8	1957.2	1917.8	1122.5	8002.3
León	0.1	168.3	180.1	1072.9	1421.4	0.0	0.0	0.5	295.3	295.8
Palencia	124.8	2416.7	1626.1	1346.1	5513.7	22.9	801.9	2185.0	2945.5	5955.2
Segovia	1234.3	1184.1	765.9	1726.4	4910.7	1443.6	1604.7	1494.7	892.9	5435.9
Soria	3116.2	2798.1	1827.6	1254.9	8996.9	3462.5	2385.9	2405.9	1168.7	9423.0
Valladolid	0.0	5.7	328.9	1083.2	1417.7	59.7	734.8	828.9	1008.8	2632.3
Castilla y León	6853.2	10343.4	6448.8	7896.7	31542.1	7993.5	7484.5	8897.4	7957.7	32333.1

extramarginal, and the latter spreads out zones of low and medium potentiality over the southwest of Palencia (Cerrato plateau) and the Torozos Range (Valladolid), while FPI labels these places as extramarginal. These are the only places where one index predicts extramarginality and the other does not.

Furthermore, according to FPI the most suitable places for *J. thurifera* in the province of Palencia are situated in the northern half and more rarely in the southeast, whereas API only defines the Cerrato plateau as highly suitable. In the province of Segovia, the factorial index predicts high and optimum potentiality over the lower elevations of the Central range of mountains, while the additive index identifies the eastern third of the province as optimum. Moreover, most of the optimum potential areas are concentrated, according to API, in the provinces where the current Spanish juniper woodlands are vaster (Soria, Burgos and Segovia). It is also noteworthy that in two watersheds (between the Ebro and eastern Duero basins, and between the western and eastern Duero basins), where the climatic models change, FPI predicts sudden transitions from the optimum potentiality class to extramarginality, which is greatly undesirable. This liability is avoided with the use of API.

In any case, it is essential to remember that the potentiality we are referring to here is only physiographic and climatic; thus, the nearly 7×10^5 or 8×10^5 ha (depending on the index) of optimum suitability area are likely to be further reduced if edaphic variables are considered.

Evaluation through current vegetation

A total of 5,221 and 5,250 plots of the 3NFI were found to be situated inside the Spanish juniper potential areas, according to API and FPI respectively. Table 3 shows the percentage of plots, by dominant species, occupying the different potentiality classes for both indexes. Taxa comprising less than 3% have been gathered in a single group

labeled “other species” (where the most frequent turned out to be the stone pine, *P. pinea* L.).

According to API, four species (*P. pinaster* Ait., *Quercus ilex* L. ssp. *ballota* (Desf.) Samp., *Q. pyrenaica* Willd. and *P. sylvestris*) exceed *J. thurifera* in number of plots occupying its potential areas. Nevertheless, only the Mediterranean maritime pine (*P. pinaster*) has a higher percentage (25.5) of occupation than the Spanish juniper (20.4) in the optimum potential areas; besides, the latter is particularly rare in the medium and low potentiality classes and is the only taxon which chiefly occupies the optimum class. This pattern is at odds with FPI, as the Holm oak also surpasses the Spanish juniper in the optimum class and the latter is quite frequent in the low and medium potentiality classes. Moreover, the other two species of the genus *Quercus* considered in the analysis (*Q. pyrenaica* and *Q. faginea* Lamk.) also have the optimum class as the most frequent. Another outstanding difference between both indexes is the number of plots dominated by *P. sylvestris* occupying the optimum potentiality class, since according to API it is 341 and according to FPI only 73.

Evaluation through climax vegetation

The list of vegetation series located in the potential physiographic and climatic areas for Spanish juniper in Castilla y León is reported in Table 4. Only six of them belong to the Eurosiberian Region, three of which are extremely reduced in area for FPI and absent for API (*Junipero nanae–Vaccineto ulginosi*, *Daphno cantabricae–Arctostaphyleto uva-ursi* y *Luzulo henriquesii–Betuleto celtibericae*); the other 15 series belong to the Mediterranean Region. According to the vegetation formations grouping exposed in Table 4, the area and percentage occupied by each one in the four potentiality classes (for both indexes) is presented in Tables 5 and 6. It is conspicuous that Holm oak formations cover the largest area (around 13,000 km² (40.4%) and 11,000 km² (35.4) for

Table 3 Percentage of plots of the 3rd NFI, by dominant species, occupying the physiographic and climatic potential areas of *J. thurifera* in the region of Castilla y León

Potentiality class	<i>Pinus pinaster</i>	<i>Quercus ilex</i>	<i>Quercus pyrenaica</i>	<i>Pinus sylvestris</i>	<i>Juniperus thurifera</i>	<i>Pinus nigra</i>	Other species	<i>Quercus faginea</i>	<i>Populus nigra</i>
FPI									
Optimum	21.39	19.31	16.83	5.85	17.39	7.45	2.16	7.61	2.00
High	16.41	17.96	14.24	17.65	12.38	10.77	1.86	4.89	3.84
Medium	15.06	17.96	13.19	18.07	11.42	7.27	5.19	7.58	4.47
Low	27.74	13.13	14.04	15.45	4.78	2.04	15.66	2.95	4.21
Total	20.42	16.93	14.61	14.32	11.33	6.97	6.29	5.50	3.62
Potentiality class	<i>Pinus pinaster</i>	<i>Quercus ilex</i>	<i>Pinus sylvestris</i>	<i>Quercus pyrenaica</i>	<i>Juniperus thurifera</i>	<i>Pinus nigra</i>	Other species	<i>Quercus faginea</i>	<i>Populus nigra</i>
API									
Optimum	25.49	12.24	16.25	11.72	20.39	5.81	1.76	4.43	1.91
High	27.77	14.79	10.23	13.76	12.55	2.92	5.93	7.48	4.56
Medium	19.24	25.66	9.15	9.36	2.42	3.47	16.30	8.83	5.57
Low	19.64	14.98	18.06	15.48	0.10	15.67	5.85	3.87	6.35
Total	23.73	15.78	13.96	12.47	11.45	6.65	6.13	5.80	4.02

FPI factorial potentiality index, API additive potentiality index

Table 4 Vegetation series located in the physiographic and climatic potential areas for Spanish juniper in the region of Castilla y León, grouped by plant formations (FPI, factorial index; API, additive index)

Vegetation series	Plant formation	Region	FPI	API
<i>Junipero nanae–Vaccineto ulginosi</i>	High mountain juniper woodlands	E	X	–
<i>Daphno cantabricae–Arctostaphyleto uva-ursi</i>	High mountain juniper woodlands	E	X	–
<i>Luzulo henriquesii–Betuleto celtibericae</i>	<i>Q. robur</i> and <i>Q. petraea</i> oakwoods	E	X	–
<i>Linario triornithophorae–Querceto pyrenaicae</i>	<i>Q. pyrenaica</i> oakwoods	E	X	X
<i>Cephalanthero longifoliae–Querceto rotundifoliae</i>	Holmoakwoods	E	X	X
<i>Junipero nanae–Cytiseto purgantis</i>	High altitude broom brush	M	X	X
<i>Junipereto sabino–thuriferae</i>	Spanish juniper woodlands	E	X	X
<i>Junipereto hemisphaerico–thuriferae</i>	Spanish juniper woodlands	M	X	X
<i>Galio rotundifolii–Fageto</i>	Beechwoods	M	X	X
<i>Ilici–Fageto</i>	Beechwoods	M	X	X
<i>Luzulo forsteri–Querceto pyrenaicae</i>	<i>Q. pyrenaica</i> oakwoods	M	X	X
<i>Holco mollis–Querceto pyrenaicae</i>	<i>Q. pyrenaica</i> oakwoods	M	X	X
<i>Festuco heterophyllae–Querceto pyrenaicae</i>	<i>Q. pyrenaica</i> oakwoods	M	X	X
<i>Cephalanthero longifoliae–Querceto fagineae</i>	<i>Q. faginea</i> oakwoods	M	X	X
<i>Epipactido helleborines–Querceto fagineae</i>	<i>Q. faginea</i> oakwoods	M	X	X
<i>Junipero thuriferae–Querceto rotundifoliae</i>	Evergreen oakwoods	M	X	X
<i>Bupleuro rigidi–Querceto rotundifoliae</i>	Evergreen oakwoods	M	X	X
<i>Spiraeo hispanicae–Querceto rotundifoliae</i>	Evergreen oakwoods	M	X	X
<i>Junipero oxicedri–Querceto rotundifoliae</i>	Evergreen oakwoods	M	X	X
<i>Genisto hystricis–Querceto rotundifoliae</i>	Evergreen oakwoods	M	X	X
<i>Riparian series</i>	Riparian formations	M	X	X

E Eurosiberian region, M mediterranean region

API and FPI, respectively) of the potentially suitable area for *J. thurifera* in Castilla y León in all classes. In second place, the *Q. faginea* forests occupy 31% of the suitable area, mainly within the high and medium classes (both

indexes). Thirdly, the area covered by vegetation series of *Q. pyrenaica* is up to 5,600 km² (17.4%) and 7,000 km² (22.0%) (API and FPI), in all potentiality classes. The two series including *J. thurifera* woodlands (*Junipereto sabino–*

Table 5 Area (km²) of each physiographic and climatic potential areas occupied by the different plant formations

Plant formation	FPI					API				
	Optimum	High	Medium	Low	Total	Optimum	High	Medium	Low	Total
<i>Evergreen oakwoods</i>	2182.8	3481.1	2237.8	3255.0	11156.7	3652.7	2844.5	3349.4	3200.5	13047.1
<i>High mountain juniper woodlands</i>	0.0	0.0	0.0	0.8	0.0	–	–	–	–	–
<i>Beechwoods</i>	2.1	6.2	15.5	417.6	441.5	4.8	18.7	22.2	22.3	67.9
<i>Q. pyrenaica oakwoods</i>	1635.2	2552.4	1237.2	1528.4	6953.2	1955.0	1177.6	610.1	1881.5	5624.9
<i>High altitude broom brush</i>	3.4	1.0	0.0	0.0	6.3	0.0	3.7	0.9	0.0	6.5
<i>Q. faginea oakwoods</i>	2014.2	3364.2	2299.7	2015.5	9693.5	730.5	2749.5	4168.5	2188.6	9837.0
<i>Q. robur and Q. petraea oakwoods</i>	0.0	0.0	0.0	30.0	31.5	–	–	–	–	–
<i>Spanish juniper woodlands</i>	955.4	645.3	379.1	189.5	2169.5	1602.6	497.5	48.0	14.3	2162.7
<i>Riparian formations</i>	60.3	291.6	276.6	457.1	1087.9	47.2	190.0	694.6	647.6	1580.8

FPI factorial index, API additive index

Table 6 First line: percentage of each physiographic and climatic potential area class for *J. thurifera* occupied by the different plant formations (percentage of row in Table 5). Second line: percentage of

each plant formation in a given physiographic and climatic potential area (percentage of column in Table 5)

Plant formation	FPI					API				
	Optimum	High	Medium	Low	Total	Optimum	High	Medium	Low	Total
<i>Evergreen oakwoods</i>	19.6	31.2	20.1	29.2	100.0	28.0	21.8	25.7	24.5	100.0
	31.9	33.7	34.7	41.2	35.4	45.7	38.0	37.7	40.2	40.4
<i>High mountain juniper woodlands</i>	0.0	0.0	0.0	100.0	100.0	–	–	–	–	–
	0.0	0.0	0.0	0.0	0.0	–	–	–	–	–
<i>Beechwoods</i>	0.5	1.3	3.5	94.7	100.0	6.5	27.4	33.3	32.8	100.0
	0.0	0.1	0.2	5.3	1.4	0.1	0.2	0.3	0.3	0.2
<i>Q. pyrenaica oakwoods</i>	23.5	36.7	17.8	22.0	100.0	34.8	20.9	10.8	33.5	100.0
	23.9	24.7	19.2	19.4	22.0	24.5	15.7	6.9	23.7	17.4
<i>High altitude broom brush</i>	65.2	29.9	4.9	0.0	100.0	0.0	73.3	26.7	0.0	100.0
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Q. faginea oakwoods</i>	20.8	34.7	23.7	20.8	100.0	7.4	28.0	42.4	22.2	100.0
	29.4	32.5	35.7	25.5	30.7	9.1	36.7	46.9	27.5	30.4
<i>Q. robur and Q. petraea oakwoods</i>	0.0	0.0	0.0	100.0	100.0	–	–	–	–	–
	0.0	0.0	0.0	0.4	0.1	–	–	–	–	–
<i>Spanish juniper woodlands</i>	44.0	29.7	17.5	8.7	100.0	74.1	23.0	2.2	0.7	100.0
	13.9	6.2	5.9	2.4	6.9	20.1	6.7	0.5	0.2	6.7
<i>Riparian formations</i>	5.5	26.9	25.5	42.1	100.0	3.0	12.0	44.0	41.0	100.0
	0.9	2.8	4.3	5.8	3.4	0.6	2.5	7.8	8.1	4.9

FPI factorial index, API additive index

thuriferae and *Junipereto hemisphaerico-thuriferae*) only comprise 7% of the physiographic and climatic potential area. The pattern found for the current vegetation comes up here again: as the potentiality decreases, the differences between classes are much broader according to API than to FPI. Thus, the former predicts 160,000 ha of Spanish juniper woodlands as climax vegetation in the optimum potentiality class (74.1% for this formation) and only 1,500

in the low (0.7%), while according to FPI the difference narrows to 95,000 (44.0%) as opposed to 19,000 (8.7%).

Finally, the noticeable increase in the riparian vegetation occupying potential areas of *J. thurifera* if API is used is remarkable. This fact ensues from the ability of this index to include flat areas, close to the main courses of water. Conversely, FPI systematically excludes such zones, as the lower limit of the parameter SLP is 2.1%.

Discussion

The adaptation of the EFT has allowed us to introduce improvements in the quantification of the potentiality of the territory. First, the prominence given to observations (instead of parameters) supports the whole analysis on current and documented facts, as do the places (real or parametric) where the species live.

Secondly, our approach overcomes the shortcoming found in FPI regarding the outwardly multivariate way of tackling the problem of ecological resemblance. Thus, if only one (or a few) of the parametric values is far from the central or even the marginal habitat, it does not mean that such a particular place must be relegated by API to extramarginality. Conversely, FPI would exclude it from the potentiality area, as it does not consider likely compensation phenomena among parameters (Rubio and Sánchez Palomares 2006). Moreover, in our approach these parametric interplays are managed with the Mahalanobis' distance, which allows the preclusion of those sites whose parametric vector differs, even if slightly, from the general trend identified by the correlation matrix, from the high potentialities. This fact is particularly outstanding in the case of the habitat of the Spanish juniper in Castilla y León, showing strong correlations among climatic parameters (Alonso Ponce 2008).

Thirdly, two advantages can be drawn from the additive character of API. On the one hand, it is feasible to reward those regions of the parametric space that are more crowded with observations: it seems to be sensible surmising that such a situation is an outcome of better suitability for the studied species. And on the other hand, it is possible, using a well-defined function as Eq. 2 is, to reduce the contribution to the ecological potential due to observations away from the cloud of points defining the parametric habitat.

These two features, along with considering the lack of the parametric space's orthogonality by using the Mahalanobis' distance, represent three advantages with regards other similar habitat distribution models belonging to the environmental envelopes group. Thus, in well-known procedures such as BIOCLIM (Busby 1991), HABITAT (Walker and Cocks 1991) or DOMAIN (Carpenter et al. 1993) the same weight is given to each observation defining the habitat, irrespective of their marginality, and the anisotropy of the distance in the non-Euclidean parametric space is not taken into account.

From a computational standpoint, calculation of API is more complex than BIOCLIM, similar to FPI or DOMAIN, which uses Gower's metric in the Euclidean space (Legendre and Legendre 1998), but clearly simpler than the convex hull method of HABITAT, which is in practice not feasible for three-dimensional spaces or over (García

López and Allué 2003). As a rule of thumb, in our 19-dimensional parametric space, and a habitat defined by 883 observations, a computer with a 3.4 GHz processor and 2 GB RAM calculated 275,000 records/h.

The conceptual framework where our method is included (environmental envelopes based on presence data) is highly recommended for disturbed ecosystems as those found throughout Castilla y León, where the studied species has conceivably a reduced distribution area due to human perturbations and therefore absence data are very likely to include a proportion of false absence records, which is obviously an undesirable drawback (Robertson et al. 2003). Furthermore, such an approach, based on species' fundamental niche, probably produces "overpredicted" suitability areas which, far from a liability, allows for comparing potential and realized distributions (Anderson et al. 2003).

In terms of *J. thurifera*, the huge expanse classified as suitable for the species in Castilla y León (more than 3 million hectares) shows up the importance that this tree should have on reforestation planning in the region. The fact that only physiographic and climatic variables are taken into consideration forces the completion of the study of each particular site with edaphic information. Despite this, the wide range of soil conditions suitable for Spanish juniper (Gauquelin and Dagnac 1988; Gauquelin et al. 1999; Alonso Ponce 2008) permits us to postulate that we are unlikely to find large tracts within the potential areas with soils that are not appropriate for the species.

The features of API are able to include the current sites dominated by the species in the optimum class of potentiality, as well as to produce a smoother transition between classes and to extramarginality than FPI does. Another example of the dissimilar results of both indexes is behavior in the neighborhood of the main courses of water. The drop-off both in ALT and SLP in such areas brings about a dramatic decrease in the value of FPI and therefore in their potentiality, even though they can be surrounded by terrains of optimum or high potentiality. This attribute gives rise to undesirable discontinuities in maps of potentiality as well as it prevents current sound Spanish juniper woodlands from being included even in the low potentiality class; a symmetrical effect is found in the summits of medium-altitude ranges. This disadvantage is overcome by API to a great extent.

The evaluation through the current vegetation shows that *P. pinaster* is the most coincident taxon with *J. thurifera* from a physiographic and climatic point of view. Nevertheless, the lack of edaphic (mainly textural) variables in the analysis can have a great influence on the result, since the Mediterranean maritime pine inhabits chiefly sandy soils of the province of Soria and Segovia. Thus, while in the former it is relatively common to find

Spanish juniper-Mediterranean maritime pine mixed stands, in the latter, where the summer drought is longer and more intense, the association between these two taxa is almost anecdotal. Regarding the overlap of current distribution areas of *Quercus* spp. with potential areas of *J. thurifera*, the two main taxa are the Holm oak and the *Q. pyrenaica* oak. Notwithstanding, current contact between *J. thurifera* and *Q. pyrenaica* is quite scarce (Costa Tenorio et al. 1997); hence, it is probably soil quality rather than climate that determines the actual disassociation between the two taxa.

Nonetheless, from a phytosociological perspective it is the *Q. faginea* forests and not the *Q. pyrenaica* forests that are the second most frequent formations covering potential Spanish juniper areas. In any case, the highlight in the comparison of the parametric and the sigmatist approach to the potentiality of *J. thurifera* woodlands is the lack of agreement. Hardly 7% of the predicted potential area is occupied by any of the two vegetation series included in the formation “Spanish juniper woodlands”. However, one of the most extensive series, *Junipero thuriferae–Querceto rotundifoliae* comprises supramediterranean Holm oak-Spanish juniper mixed stands. Thus, if the latter were considered as Spanish juniper woodland, this formation would comprise the most common vegetation form occupying the physiographic and climatic potential area of the species. This hesitation in assigning Spanish juniper woodlands to one phytosociological series or another is a direct outcome of the lack of originality of their associated flora (Costa Tenorio et al. 1996).

Conclusions

The novel methodology to develop predictive habitat distribution models, based on the EFT, has permitted us to overcome the liability of the strong correlation between ecological parameters, as well as to take into account the position of the observations defining the habitat in the parametric space. Thus, observations located near the center of gravity of the cloud of points create stronger potentials, at a same distance, than those situated in remote areas of the parametric space. Testing the methodology on the habitat distribution of *J. thurifera* in the region of Castilla y León, smooth transitions between potentiality classes are accomplished, and most of the current Spanish juniper woodlands are included in the optimum and high potentiality classes, which comprise more than 1.5 million ha. Finally, it must be stressed again that in this work only physiographic and climatic potentiality are considered.

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