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Phytoclimatic versatility and potential diversity of natural arboreal forest cover in peninsular Spain

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Abstract

A multivariate methodology was assayed to evaluate the phytoclimatic versatility of peninsular Spain and how this relates to the potential diversity of natural tree covers. The instances of greatest phytoclimatic versatility occur in a range of altitude between 1000 and 1300 m; these are cool phytoclimates with only short, low-intensity periods of aridity. These factorial ambits of maximum versatility correspond chiefly to the substeppe nemoral subtype VI(VII), followed by genuine nemoral VI and humid nemoromediterranean $VI(IV)_2$ subtypes. The lowest values of versatility and potential diversity correspond to dry genuine Mediterranean (IV_i) or transitional Mediterranean $IV(VI)_1$ subtypes and to alpine oroborealoid or oroarcticoid subtypes. In geographical terms, intermediate mountain areas in the north of the Peninsula and some massifs in the southern half score the highest in the Diversity Index used. The lowest scores are found in the southern half of the Peninsula, although in the northern half low scores are also found for littoral areas, interior areas of the Duero and Ebro basins and alpine areas. Autoecological phytoclimatic spectra headed by stands of *Pinus nigra* and *Quercus petraea* present the greatest phytoclimatic versatility, while those headed by *Quercus ilex ballota* and *Pinus uncinata* stands present the least versatility. This article offers new methodological horizons for the study of the effects of climate change on plant diversity.

Key words: Biodiversity, suitability, competition, climate change, Simpson Index.

Resumen

Polivalencia fitoclimática y diversidad potencial de cubiertas forestales arbóreas naturales en la España peninsular

Se ensaya una metodología multivariante de evaluación de la polivalencia fitoclimática de la España peninsular y de su relación con la diversidad potencial de las cubiertas arbóreas naturales. Las mayores polivalencias fitoclimáticas se dan en una franja altitudinal situada entre los 1000 y los 1.300 m, correspondiendo a ámbitos fitoclimáticos frescos y con escasa duración e intensidad de la aridez. Estos ámbitos factoriales de máxima polivalencia se corresponden principalmente con el subtipo nemoral subestepario VI(VII), seguido del nemoral genuino VI y del nemoromediterráneo húmedo $VI(IV)_2$. Los menores valores de polivalencia y de diversidad potencial se corresponden con subtipos mediterráneos genuinos (IV_i) o transicionales $IV(VI)_1$ secos y con subtipos oroborealoides u oroarticoides de alta montaña. Desde un punto de vista geográfico, las zonas de media montaña de la mitad norte peninsular y algunos macizos montañosos de la mitad sur dan los valores más altos del Índice de Diversidad utilizado, mientras que los menores se dan en la mitad sur peninsular, aunque en la mitad norte las áreas litorales, las áreas interiores de las cuencas del Duero y Ebro así como y en las áreas de alta montaña también se corresponden con valores bajos del índice. Los espectros fitoclimáticos de carácter autoecológico encabezados por pinares de *Pinus nigra* y por robledales de *Quercus petraea* presentan la mayor polivalencia fitoclimática, mientras que los encabezados por encinares de *Quercus ilex ballota* y por pinares de *Pinus uncinata* presentan la menor. El presente trabajo abre nuevos horizontes metodológicos para el estudio de los efectos del cambio climático sobre la diversidad vegetal.

Palabras clave: Biodiversidad, idoneidad, competencia, cambio climático, Índice de Simpson.

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Introduction

Biodiversity estimation has acquired increasing importance over the last few decades as a key tool for nature management. Aspects such as the evaluation of an area for the purpose of taking legal and administrative steps to protect it, assessment of the possible impacts of plans, programmes or projects, or the taking of decisions in the light of future uncertainties surrounding climate change, are all largely founded upon methodologies for the estimation of ecological diversity. Indeed, the effects of climate change on the diversity of plant covers and on internal competitive relationships among the principal species constituting those covers seems likely to be one of the priority lines of research in the future (Fernández-González *et al.*, 2005).

It is also the case that the ecological characterization of the environment in which a forest species grows is highly important for the purpose of managing natural populations. Studies of this kind have a number of applications. These include: determination of the most suitable resources for use in the reconstruction of forest cover; identification of sites which in principle appear suitable for practical application of the results of preliminary experiments in the localities of origin; identification of possible interfering factors; definition of programmes for the conservation of genetic resources of representative, scarce or endangered species or populations; and the identification of environmental factors presumably responsible for intraspecies variation or for the principal genotype/environment interactions of these species.

From a phytoclimatic standpoint the potential of an area of land to host different types of arboreal forest cover can be studied holistically using mathematical models to determine what principal species of a forest formation are compatible with that area, and also the degree of adjustment of each of these formations to the phytoclimatc environment at the station concerned.

This integrated phytoclimatic approach not only provides a means of determining the potential wealth of an area in terms of arboreal forest formations, assessed on the basis of the number of compatible principal species; in addition, by calculating numeric adjustment indicators it is possible to assess the capacity of the medium to host each forest formation, and from there to enter the complex universe of competitive relationships between species and between forest formations by comparing their relative degrees of adjustment. The importance of the competition factor in the distribution of plant species is such that according to some authors (Walter, 1977), the natural limits of distribution of a species will occur where its ability to compete is so depleted by variable environmental conditions that it is supplanted by other species; generally speaking, ecological factors are only decisive at the absolute limits of distribution. Along with the phytoclimate, competition with other arboreal forest taxa is usually identified as a major factor governing the distribution of *Quercus* formations in the Iberian Peninsula (Soriano *et al*., 2004).

This last aspect is vitally important for an accurate assessment of the diversity of these tree covers, as it actually comprises two elements: the wealth or number of elements studied, and the relative proportions of these elements (Magurran, 1989). Aspects relating to the influence of inter-species dominance and diversity are widely dealt with in the specialized literature (Whittaker, 1965), but not from a phytoclimatic perspective.

Thanks to its size and geographic situation, the Iberian Peninsula possesses one of the most diversified forest stocks in the European Union. In this work we assayed a methodology for evaluating the potential diversity of tree covers in peninsular Spain, based on multivariate phytoclimatic models. This article attempts to provide answers to such questions as what geographical areas of peninsular Spain are the most diversified, what factorial ambits and phytoclimatic subtypes are best suited to the occurrence of high diversity values, and what are the chief factors responsible for the distribution of that diversity. It also includes an attempt at a preliminary cartographic approximation.

Material and Methods

From the data base of sampling parcels defined in the Second National Forestry Inventory (DGCONA 1986-1995), 35,767 points were selected in which 16 arboreal forest species were the principal forest formation species in peninsular Spain. Parcels were selected using an IT utility called BASIFOR (Del Río *et al.*, 2001) and setting apart all registers in which each species occurred naturally as the first dominant species in the formation. Table 1 shows the distribution by species of the 35,767 sampling points used and their codes. Figure 1 shows their geographic distribution.

Pinus pinaster, *Pinus pinea* and *Pinus halepensis* were not taken into consideration for purposes of this assay due to problems of discrimination between natural and artificial formations which need to be conside-

Table 1. Codes and number of sampling points of species used in the construction of the phytoclimatic system

Code	Species	Stations	Code	Species	Stations
Pni	*Pinus nigra*	2,805	**Qba**	*Quercus ilex ballota*	13,581
Psy	*Pinus sylvestris*	4,942	**Qil**	*Quercus ilex ilex*	1,043
Pun	*Pinus uncinata*	536	**Qsu**	*Quercus suber*	2,055
Api	*Abies pinsapo*	10	**Qca**	*Quercus canariensis*	90
Aal	*Abies alba*	162	**Qfa**	*Quercus faginea*	1,855
Fsy	*Fagus sylvatica*	1,795	**Qpy**	*Quercus pyrenaica*	3,390
Qro	*Quercus robur*	1,687	**Qhu**	*Quercus humilis*	52
Qpe	*Quercus petraea*	666	**Jth**	*Juniperus thurifera*	1,098

red in more detail. These will be the subject of future study.

The 35,767 sampling points were identified by their UTM coordinates (UTM Zone 30) and their altitude and were processed with the FITOCLIMOAL programme (García-López and Allué, 2000) to obtain gross monthly temperature and precipitation data according to the regionalized thermopluviometric estimation models of Sánchez-Palomares *et al*. (1999). Subsequently, the same programme was used to identify the values of the 12 phytoclimatic factors in table 2. The extreme values of the factorial ambits for each species are shown in table 3.

The phytoclimatic system used is based on the models of Allué-Andrade (1990 and 1997) as modified by García-López and Allué Camacho (2003). With this phytoclimatic system is possible not only to fit a station into a previously-defined phytoclimatic category in qualitative terms but also to quantify the adjustment of the station to that category or phytoclimatic type, and likewise all the other types in the system, using relative "*position coordinates*" and "*phytoclimatic distances*", between these and relative to factorial phytoclimatic ambits.

Figure 1. Geographic distribution of the 35,767 sampling points for the tree species used in the construction of the autoecological phytoclimatic system

Each species was assigned an autoecological factorial ambit, defined on the basis of the corresponding sampling points. According to García-López and Allué Camacho (2003), the borderline of each ambit can be defined in very close correspondence with the cluster of points in 12-dimensional factorial hyperspace by calculating a convex envelope that will convert it to a hyperpolyhedron and can be projected on to planes formed by pairs of factors in order to perform the specific calculations for the phytoclimatic model.

The geographical basis on which the phytoclimatic system thus constructed was applied was a factorial data base generated from the digital model of elevations in the Iberian Peninsula known as GTOPO30, from the US Geological Survey, with a resolution of approximately 1 km per side, following preliminary treatment by FITOCLIMOAL'2000 to find the value of the phytoclimatic factors for each point. This model consists of approximately 500,000 geographical points identified by their UTM zone 30 coordinates and their altitude.

The diagnosis of the 499,947 points in the factorial data base for peninsular Spain using the autoecological phytoclimatic system of principal tree species produced a set of diagnostic spectra with an abbreviated annotation of the following type:

$$\mathbf{(e_a.A;\ e_b.B;\ e_c.C;\ e_d.D;\ldots\ldots\ldots\ e_i.I)}$$

for i=16 species, where A, B, C, D …I are the abbreviated codes (table 1) for the species, inside whose phytoclimatic

Table 2. Phytoclimatic factors used

ABBREVIATION	FACTOR	UNIT
K	Intensity of aridity. Calculated on the basis of the quotient As/Ah, where Ah is the humid area of the climodiagram (Pi curve above the Ti curve, i.e., 2Ti<Pi) and As is the dry area of the climodiagram (Pi curve below the Ti curve, i.e., 2Ti>Pi).	
A	Duration of aridity in the sense of GAUSSEN, that is the number of months in which the Ti curve is above the Pi curve, i.e., 2T1>Pi.	months
P	Total annual precipitation	mm
PE	Minimum summer precipitation (June, July, August or September)	mm
TMF	Lowest monthly mean temperature	ºC
T	Mean annual temperature	ºC
TMC	Highest monthly mean temperature	ºC
TMMF	Average of the minima of the month with the lowest mean temperature.	ºC
TMMC	Average of the maxima of the month with the highest mean temperature.	ºC
HS	Certainty of frost. Calculated as the number of months in which Ti<=4ºC	months
PV	Period of free plant activity, calculated as the number of months in which Ti>=7.5ºC, not counting periods where A>0	months
OSC	Thermal oscillation. Calculated as TMC-TMF	ºC

ambits, defined by the convex envelope, is included the point analysed, and where ei (>=0 and <=1) is the scalar of adjustment of the target station to the phytoclimatic ambit of species i, with ea>eb>ec>ed>…..>ei (García-López and Allué Camacho, 2005). For example, a station whose diagnostic spectrum is (0.87.Qfa; 0.73.Jth; 0.51.Pni; 0.17.Psy) is phytoclimatically compatible with stands of *Quercus faginea*, *Juniperus thurifera*, *Pinus nigra* and *Pinus sylvestris*, in descending order of adjustment to the site. In fact each scalar functions as an index of phytoclimatic suitability of a forest species with respect to the optimum.

For the purposes of this article, "phytoclimatic suitability" (Allué Camacho, 1996) means the degree to which a site is suited to host certain taxa or syntaxa, principally in terms of staying power (self-regenerating capacity), ability to compete with other species and resistance to diseases.

The diversity of phytoclimatically compatible arboreal forest covers was estimated using an indicator that takes into account the two basic components of the concept, namely wealth and relative proportionality. A given station will present high diversity when not only is there a large number of principal tree species compatible with that station (wealth) but also all these compatible covers present a high level of adjustment to the station (proportionality), without any one species predominating excessively over the rest.

To estimate the diversity of each of the 499,947 stations considered, we used Simpson's proportional abundance index (Simpson, 1949), hereafter "Sim", multiplied by 100 for convenience of scale; this is one of the most commonly used indices in estimations of this kind (Magurran, 1989):

$$\mathbf{Sim = 100.(1/\sum [e_i.(e_i-1)/E.(E-1)]) \text{ with } E = \sum e_i}$$

By way of example, in the case of the station cited above, a phytoclimatic diagnostic spectrum (0.87.Qfa; 0.73.Jth; 0.51.Pni; 0.17.Psy), compatible with 4 forest formations but presenting a strong imbalance of adjustments between the best-adjusted species (*Quercus faginea*) and the least adjusted species (*Pinus sylvestris*) would give a Sim=333, while another station with the same number (wealth) of compatible species but a better balance of adjustments, e.g. (0.87.Qfa; 0.85.Jth; 0.80.Pni; 0.79.Psy), would give a Sim=403. Even a station with fewer species than another may give a higher Sim value than the latter if it presents a better balance of phytoclimatic adjustments. Compare for instance a station with a phytoclimatic diagnostic spectrum (0.87.Qfa; 0.37.Jth; 0.31.Pni; 0.17.Psy), compatible with 4 forest formations but presenting a strong imbalance of adjustments, with a Sim=294, and a station having only 3 compatible forest formations with a diagnostic spectrum (0.87.Qfa; 0.86.Jth; 0.85.Psy), which would have a Sim=300. The compromise between wealth and balance has been widely dealt with in the specialized literature from various different perspectives (May, 1973; Pimm, 1984).

Table 3. Phytoclimatic ambits of the species used in the construction of the autoecological phytoclimatic system. Each cell shows, from top to bottom, the upper and lower limits of the factorial ambit and in brackets the standard error of estimation calculated from 803 meteorological stations with at least 20 years of monitoring within the base period 1940-1989 in which thermopluviometric estimation models were constructed

Code	K	A	P	PE	T	TMF	TMC	TMMF	TMMC	HS	PV	OSC
Pni	0.161	3.32	1325	46	11.6	3.9	22.2	0.1	27.9	5.4	8.2	19.6
	0	0	503	4	6.7	-0.4	14.6	-3.9	19.9	0.6	3.6	13.4
	(0,148)	(0,457)	(109,101)	(3,839)	(0,719)	(0,771)	(0,962)	(1,099)	(1,306)	(0,587)	(0,751)	(0,991)
Psy	0.071	2.50	2337	114	10.9	3.7	20.7	0	26.3	6.3	8.2	18.7
	0	0	525	8	4.2	-2.5	12.3	-5.9	17.6	2.1	2.8	12.2
	(0,128)	(0,485)	(112,937)	(6,382)	(0,692)	(0,779)	(0,917)	(1,079)	(1,240)	(0,620)	(0,704)	(0,957)
Pun	0	0	2117	116	7.4	1.1	16.7	-2.5	22.6	7.0	5.7	17.1
	0	0	734	43	2.6	-3.8	10.0	-7.1	15.6	4.4	3.0	13.1
	(0,113)	(0,483)	(115,048)	(8,321)	(0,647)	(0,807)	(0,891)	(1,131)	(1,253)	(0,614)	(0,651)	(1,022)
Api	0.092	3.13	2384	10	13.6	7.1	22.5	3.1	27.5	0	7.9	15.4
	0.02	1.60	1154	4	11.0	4.8	19.6	1.0	24.7	0	5.1	14.8
	(0,098)	(0,375)	(152,587)	(1,518)	(0,802)	(0,990)	(0,973)	(1,407)	(1,230)	(0,000)	(0,515)	(0,953)
Aal	0	0.00	2442	108	8.9	2.6	18.5	-1.1	24.4	6.0	6.4	17.7
	0	0	754	52	4.6	-1.9	12.6	-5.3	18.2	3.2	4.2	13.8
	(0,112)	(0,496)	(115,794)	(9,610)	(0,649)	(0,875)	(0,846)	(1,221)	(1,249)	(0,605)	(0,705)	(1,048)
Fsy	0.024	1.59	2417	120	11.0	5.3	20.1	1.5	25.8	5.8	8.4	17.6
	0	0	606	18	5.3	-1.2	12.6	-4.6	17.6	0	4.0	11.8
	(0,110)	(0,488)	(149,335)	(8,135)	(0,685)	(0,822)	(0,896)	(1,155)	(1,253)	(0,615)	(0,734)	(0,986)
Qro	0.026	1.75	2220	115	14.5	9.1	21.1	5.0	26.4	1.1	12.0	15.8
	0	0	805	23	10.0	3.6	15.8	-0.1	20.0	0	6.5	8.9
	(0,057)	(0,505)	(184,539)	(9,632)	(0,650)	(0,833)	(0,823)	(1,229)	(1,257)	(0,412)	(0,816)	(0,997)
Qpe	0.011	1.36	1958	103	13.0	6.6	21.7	2.7	27.1	5.2	9.0	18.2
	0	0	760	24	6.3	-0.7	13.9	-4.2	19.2	0	4.6	11.6
	(0,104)	(0,490)	(158,364)	(8,731)	(0,660)	(0,799)	(0,890)	(1,137)	(1,239)	(0,564)	(0,716)	(0,986)
Qba	1.341	6.67	2330	99	18.6	12.5	28.2	8.2	33.8	4.5	9.9	21.4
	0	0	310	0	8.0	0.3	15.5	-3.2	20.5	0	3.1	11.6
	(0,130)	(0,452)	(135,073)	(6,596)	(0,712)	(0,874)	(0,930)	(1,134)	(1,233)	(0,506)	(0,883)	(1,037)
Qil	0.628	4.84	1864	98	18.5	12.3	28.0	8.0	33.5	0	12.0	20.3
	0	0	509	0	13.0	4.5	19.8	0.7	24.5	0	5.7	12.4
	(0,043)	(0,510)	(210,393)	(10,894)	(0,632)	(0,884)	(0,790)	(1,343)	(1,257)	(0,321)	(0,893)	(1,083)
Qsu	0.255	4.02	1530	4	17.7	11.8	26.1	7.5	31.2	0	9.4	16.2
	0.06	2.62	796	0	14.9	7.8	23.5	3.8	28.4	0	8.0	13.0
	(0,117)	(0,451)	(147,739)	(6,317)	(0,707)	(0,972)	(0,916)	(1,144)	(1,222)	(0,246)	(1,091)	(1,161)
Qca	0.385	3.48	1881	66	15.3	8.0	25.5	4.0	31.3	4.3	10.2	21.0
	0	0	387	4	8.1	0.7	16.2	-2.9	21.3	0	4.2	12.7
	(0,098)	(0,375)	(152,587)	(1,518)	(0,802)	(0,990)	(0,973)	(1,407)	(1,230)	(0,000)	(0,515)	(0,953)
Qfa	0.269	3.49	2354	109	16.3	8.3	26.3	4.3	32.0	5.6	11.4	20.6
	0	0	431	1	5.8	-0.6	14.2	-4.1	19.2	0	3.9	10.3
	(0,130)	(0,457)	(136,654)	(6,700)	(0,706)	(0,876)	(0,927)	(1,128)	(1,237)	(0,517)	(0,886)	(1,041)
Qpy	0.004	0.68	1775	96	14.2	7.0	22.8	3.0	28.4	4.6	9.8	18.7
	0	0	593	32	7.3	0.1	15.9	-3.4	21.3	0	5.5	11.8
	(0,123)	(0,444)	(136,990)	(6,942)	(0,706)	(0,881)	(0,928)	(1,123)	(1,218)	(0,517)	(0,898)	(1,049)
Qhu	0.710	3.80	1635	39	15.7	6.5	25.5	2.6	31.4	5.8	8.2	19.9
	0	0	404	6	5.0	-1.6	12.8	-5.0	18.4	0	4.3	14.4
	(0,107)	(0,486)	(110,945)	(9,167)	(0,654)	(0,859)	(0,848)	(1,193)	(1,234)	(0,608)	(0,697)	(1,012)
Jth	0.194	2.56	1574	104	16.0	9.9	23.9	5.8	29.5	0	12.0	19.0
	0	0	515	9	11.0	4.0	17.9	0.2	22.7	0	8.0	10.7
	(0,142)	(0,461)	(114,111)	(5,930)	(0,735)	(0,915)	(0,957)	(1,078)	(1,215)	(0,609)	(0,950)	(1,059)

Results

Table 4 shows the data derived for phytoclimatic wealth of compatible tree formations. From the 16 species considered in the construction of the phytoclimatic system, combinations of up to 8 species were obtained. Figure 3 shows the geographic distribution of this phytoclimatic wealth.

Two-thirds of the stations considered (303,266 stations) present phytoclimatic spectra with 1-2 compatible species. Stations with no compatible tree species are in alpine areas or semi-arid areas in the South-East, or in some central areas of the Ebro depression. There are only 2887 stations with outstanding wealth (7-8 compatible species); these are located preferentially in the northern Iberian system, the foothills of the eastern Cantabrian mountains and foothills of the western Pyrenees (figure 2). In geographical terms, increasing values of wealth tend to define an optimal altitudinal band between 1000 and 1300 m for phytoclimatic spectra with 8 compatible forest formations.

Table 5 shows the factorial ambits identified for the Simpson Index 100-point numeric classes considered. As the table shows, increasing Index values tend to define ever stricter factorial ambits.

Increasing values of phytoclimatic versatility tend to define thermally cool factorial ambits where aridity is short-lived and of low intensity.

Table 6 shows the values of the Pearson bilateral correlation coefficient between the Simpson Index and the 12 factors considered for the 35,767 stations studied; in all cases the coefficient was significant at a level of 0.01. The correlations confirm that the highest index values correspond to cold phytoclimates where aridity is slight and of short duration. Pluviometric factors correlate less well with the index than thermometric factors, except in the case of thermal oscillation (OSC), which correlated least well of the 12 factors considered.

Figure 2. Geographic distribution of phytoclimatic wealth of tree covers, estimated as the number of genuine forest formations included in the phytoclimatic diagnostic spectrum. Red=0-2 compatible species; orange= 3-4; green= 4-5 and blue=more than 5.

Figure 3 shows the geographic distribution of Simpson Index values, as a first cartographic approximation to the potential phytoclimatic diversity of tree covers in peninsular Spain.

As figure 3 shows, the highest Simpson Index values, and hence the greatest instances of phytoclimatic versatility are found in the mountain massifs in the northern half of the peninsula and in their foothills. The lowest index values belong to much of the southern half of the Peninsula, excepting in the main mountain massifs there. In the northern half there is also low versatility in the centre of the Ebro and Duero basins, littoral areas and alpine areas.

Table 4. Phytoclimatic wealth in compatible tree species

No of Species	Stations	Min. Alt. (m)	Max. Alt (m)
0	38,003	0	3,450
1	152,881	0	2,371
2	150,385	1	2,170
3	72,601	50	1,951
4	44,710	196	1,935
5	25,418	424	1,875
6	13,062	432	1,568
7	2,627	434	1,529
8	260	1,006	1,284

Table 5. Phytoclimatic ambits as functions of wealth in compatible tree covers

Sim	St.	Alt.	K	A	P	PE	T	TMF	TMC	TMMF	TMMC	HS	PV	OSC
<200	312.870	3450	>1000	12	3113	148	18.8	12.6	28.4	8.3	34	10.4	12	21.4
		0	0	0	105	0	-2.2	-8.4	4.9	-11.4	10.7	0	0	8.0
>=200 and <300	105.527	2170	0.655	4.83	2408	107	18.4	12.1	28	7.8	33.5	6.3	12	20.4
		1	0	0	409	0	4.3	-2.4	12.3	-5.8	17.9	0	4	10.7
>=300 and <400	46.868	1935	0.244	3.97	2210	107	17.2	10	26.1	5.9	31.9	5.9	10.3	20.2
		145	0	0	446	1	4.9	-1.6	12.9	-5.0	18.4	0	4.1	11.6
>=400 and <500	26.099	1875	0.157	3.38	1921	101	14.6	7.5	23.6	3.5	28.7	5.1	9.3	18.9
		424	0	0	530	5	6.4	-0.5	14.4	-4.0	20.0	0	4.3	12.5
>=500 and <600	13.217	1568	0.058	1.98	1716	77	12.7	5.9	21	2	26.3	4.4	8.9	18.0
		432	0	0	551	19	7.6	0.3	16.1	-3.2	21.5	0	4.6	12.8
>=600 and <700	2.654	1529	0.018	1.51	1652	67	11.6	4.9	19.4	1.1	24.9	4	8.2	17.0
		434	0	0	611	23	8.0	0.6	16.3	-3.0	22.0	0	4.7	13.0
>=700	260	1284	0.011	1.36	1448	65	9.9	2.9	18.4	-0.8	23.8	3.6	6.9	16.2
		1006	0	0	791	26	8.4	0.8	16.8	-2.8	22.5	2.4	5.1	15.4

Table 7 shows the average Simpson Index values for each of the phytoclimatic subtypes found in peninsular Spain. As we can see, the subtypes presenting the greatest potential phytoclimatic density of compatible tree covers are substeppe nemoral VI(VII) followed by genuine nemoral (VI) and humid nemoro-Mediterranean $VI(IV)_2$. The subtypes presenting the lowest values of potential diversity are dry genuine Mediterranean (IV_1, IV_2, IV_4) or transitional Mediterranean $IV(VI)_1$ and alpine oroborealoid or oroarcticoid, for instance VIII(VI), X(VIII), $X(IX)_1$ and $X(IX)_2$.

Table 8 shows the average Simpson Index values for forest formations heading the phytoclimatic diagnostic spectra. As the table shows, the greatest potential phytoclimatic diversity of tree covers is found in diagnostic spectra headed by *Pinus nigra* and by *Quercus petraea*, while the lowest versatility is found in the spectra headed by formations of *Quercus ilex ballota* and *Pinus uncinata*.

Discussion

The results of this study provide the basis for an initial approximation to such issues as which geographical areas of peninsular Spain are most diverse. They show that the highest indices of phytoclimatic versatility, as estimated with a form of the Shannon Index adapted to the phytoclimatic suitability scalars in the model used, occur in semi-mountainous areas in the northern half of the Peninsula at altitudes between 1000 and 1300 metres and in some mountain massifs in the southern half, while the lowest indices are found in the southern half of the Peninsula, in littoral areas of the northern half, in inland areas along the Duero and Ebro basins, and in alpine zones.

It also provides answers to question such as what factorial ambits are most suitable for hosting high phytoclimatic diversity values; the upper and lower numeric limits of 12 factors are estimated, and of these K, A, T, TMF and TMMF are identified as the ones correlating most closely with high versatility, so that the highest diversity indices tend to reflect cool phytoclimates (T values around 9ºC) with brief periods of aridity (A less than 1.5 months). Clearly thermic factorial situations (T>17ºC or TMF>10ºC for example), or else clearly xerophytic ones (A>4 months), are associated with low indices of phytoclimatic versatility and hence low potential phytoclimatic diversity.

The results have also made it possible to identify the phytoclimatic subtypes best suited to host high values of diversity; these are nemoral subtypes, either genuine (VI) or tending towards steppe or Mediterranean, always provided that such trends are away from thermic situations. This is true of ytansitional nemoral subtypes

Table 6. Bilateral Pearson correlation coefficient between Simpson Index values and factorial values of the 35,767 stations studied

	K	A	P	PE	T	TMF	TMC	TMMF	TMMC	HS	PV	OSC
Pearson's Correlation	-0.50	-0.44	0.16	0.27	-0.50	-0.51	-0.47	-0.51	-0.45	0.44	-0.33	-0.08

Table 7. Mean value and standard deviation of the Simpson Index (x100) as a function of the phytoclimatic subtype. Dashes denote Sim values <100

Subtype	Stations	Average Sim	ST.D. Sim
III(IV)	239	-	-
IV(III)	1,446	-	-
IV$_1$	19,275	-	-
IV$_2$	22,286	150	50
IV$_3$	6,759	120	40
IV$_4$	85,064	176	45
IV(VI)$_1$	32,462	121	43
IV(VI)$_2$	5,516	158	49
VI(IV)$_1$	119,050	177	94
VI(IV)$_2$	83,089	330	112
VI(IV)$_3$	1,213	152	73
VI(IV)$_4$	9,444	228	104
VI(VII)	34,073	349	160
VI(V)	51,575	159	92
VI	34,721	339	169
VIII(VI)	137	-	-
X(VIII)	78	-	-
X(IX)$_1$ -X(IX)$_2$	1,068	-	-
Total	**499,947**	**214**	**128**

VI(VII), VI(IV)$_1$ and VI(IV)$_2$ but not of more thermic transitionals like VI(V), VI(IV)$_3$ or VI(IV)$_4$. The least versatile subtypes are genuine Mediterranean IV$_i$ or dry transitional VI(IV)$_1$.

Figure 3. Geographic distribution of Simpson Diversity Index values for phytoclimatic compatibility of tree covers. Red= Sim<200; orange= Sim between 200 and 300; green= Sim between 300 and 400; blue=Sim between 400 and 500; violet= Sim>500.

The results indicate that the autoecological spectra headed by stands of *Pinus nigra* and *Quercus petraea* exhibit the greatest phytoclimatic versatility, while those headed by stands of *Quercus ilex ballota* and *Pinus uncinata* exhibit the least, as representatives of clearly limiting situations associated with dryness and cold respectively.

One of the primary conclusions drawn from the results relating to factorial ambits, spectra for diagnosis of phytological strategies and spectra for autoecological diagnosis of species is that the greater phytoclimatic versatility seems to be associated preferentially with stations where there are situations limiting plant growth, but always moderately. In fact values of 5 to 7 months' duration for the factor PV, which has a close bearing on these limitations, are associated with the highest indices of phytoclimatic diversity, while clearly limiting situations (PV<4 months) such as are encountered in alpine or semi-arid areas, or clearly non-limiting situations (PV>12 months) such as are encountered in lauroid-trending littoral areas are associated with low indices.

One possible interpretation of this finding is that limiting factorial situations induce greater versatility in the life strategies potentially emerging in the terrain to respond to these limitations, but that increasing demand for specialization to deal with severely limiting situations like those

Table 8. Mean value and standard deviation of the Simpson Index (x100) as a function of the first species in the phytoclimatic diagnostic spectrum

1st Species in the Spectrum	Stations	Average Sim	ST.D. Sim
Pinus nigra	39,033	454	101
Pinus sylvestris	5,117	147	58
Pinus uncinata	996	105	22
Abies pinsapo	2	172	4
Abies alba	1,295	321	78
Fagus sylvatica	6,029	277	115
Quercus robur	45,013	157	77
Quercus petraea	28,893	437	115
Quercus ilex ballota	121,165	100	1
Quercus suber	88,800	196	22
Quercus canariensis	1,177	251	45
Quercus faginea	81,944	253	56
Quercus pyrenaica	10,142	224	79
Quercus pubescens	3,758	306	69
Juniperus thurifera	27,158	329	76
Quercus ilex ilex	7,162	201	82

encountered in alpine or semi-arid areas considerably reduces the range of phytological strategies and hence the catalogue of tree species compatible with that terrain.

In short, measuring phytoclimatic versatility could be useful in the future as a means of estimating the capacity of a forest ecosystem to respond to a variety of scenarios of disturbance, as there appears to be clear relationship between such phytoclimatic versatility and the limited stock of phytological strategies available to the station as means to recovery. The results reported here, and above all the methodology assayed, could point the way for future developments in mapping the phytoclimatic vulnerability of forest ecosystems. Moreover, by comparing the catalogue of tree species present at a station with those that could potentially be present from a phytoclimatic standpoint, always bearing in mind the inevitable edaphic limitations, it should be possible to assess how capable they are of responding and hence how stable a forest ecosystem is. This in turn would facilitate the planning of forestry management policies aimed at diversifying the existing tree cover and matching the actual composition to the theoretical potential.

This work opens up new methodological horizons for the study of plant diversity from a phytoclimatic perspective. While the approach adopted to address so complex a problem is a new one within the present spectrum of studies on plant ecology, it does nonetheless present a number of limitations. The most obvious of these is that it does not take into consideration the nature of the substrates, an aspect which imposes a need for cautious interpretation of results as regards the edaphic compatibility of some species, for instance *Quercus suber* or *Quercus pyrenaica*, in basic substrates. In other instances the potentiality is masked by a long history of human land uses or geomorphological azonalities.

Also, we must draw attention to the limited number of species that are considered in the construction of the phytoclimatic system. Although the species considered include practically all those that head potential vegetation series, for the future we need to consider some species which are important in the forest landscape of peninsular Spain. These include such species as *Pinus pinaster* or *Pinus pinea*, which are widely used in reafforestation, so that for the future parcels containing artificial stands will need to be carefully screened.

Another aspect that has to be addressed in future approaches to the problem is the consideration of secondary tree species which are not actually dominant in the plant landscape of peninsular Spain but are of great ecological and diagnostic importance in its forests. This will inevitably affect the capacity and speed of the complex computer calculations needed to apply phytoclimatic models with more than 25 species, which in the present state of development of PC processors will mean that it takes several months to process an ambit with the precision that this study demands.

Table 9. Phytoclimatic diagnostic spectra of species having a Sim greater than 700

Spectrum of Species	Stations	Average Sim	ST.D. Sim
(Qpe;Fsy;Pni;Jth;Qfa;Qpy;Psy;Qba;)	12	773	0.7
(Pni;Fsy;Jth;Qpe;Qpy;Psy;Qfa;Qba;)	1	772	
(Qpe;Fsy;Pni;Qfa;Jth;Qpy;Psy;Qba;)	29	772	1.0
(Qpe;Fsy;Pni;Jth;Qfa;Psy;Qpy;Qba;)	5	771	0.5
(Pni;Fsy;Jth;Qpe;Psy;Qpy;Qfa;Qba;)	34	769	1.4
(Qpe;Fsy;Pni;Jth;Psy;Qpy;Qfa;Qba;)	1	768	
(Pni;Fsy;Qpe;Jth;Psy;Qpy;Qfa;Qba;)	71	766	1.1
(Pni;Qpe;Fsy;Jth;Psy;Qpy;Qfa;Qba;)	56	762	2.5
(Qpe;Fsy;Qhu;Psy;Aal;Qpy;Qfa;Qba;)	7	751	0.9
(Qpe;Fsy;Qhu;Aal;Psy;Qpy;Qfa;Qba;)	44	747	3.3

There is another potential limitation associated with the shortage of thermopluviometric meteorological stations with data going far enough back and their traditional remoteness from alpine forest areas. This makes it necessary to work with approximations to factorial values based on thermopluviometric estimation models. These are a primary source of errors and obviously compromise the validity of the results to a certain extent, but not the bases of the methodology as applied. They may be expected to improve with time as the available thermopluviometric estimation models are further refined.

In our final conclusions we would stress that this article offers new methodological horizons for the study of the effects of climate change on plant diversity. In particular, future estimations of factorial numeric dynamics such as possible increases of temperature or decreases of precipitation can be interpreted more efficiently with this methodology for purposes of predicting future changes in values of forest diversity, alterations to the medium's hosting capacities, and competitive relations among the principal species in a formation. All this will make it possible to perfect the mechanisms used to makes assessments and take preventive and ameliorating decisions in future scenarios of phytoclimatic uncertainty and thus achieve progress in some of the priority lines of research in this field (Gracia *et al*, 2005).

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