



Biogeographical analysis of species of the tribe Cytiseae (Fabaceae) in the Iberian Peninsula and Balearic Islands

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ABSTRACT

Aim To analyse quantitatively the biogeographical distribution pattern of species of the Cytiseae Bercht. & J. Presl (= Genisteeae Benth.) tribe in the Iberian Peninsula and the Balearic Islands, and to identify environmental variables related to the distributional patterns.

Location Iberian Peninsula and Balearic Islands, using the 61 administrative provinces as operational geographical units.

Methods In order to identify chorotypes (groups of species with similar geographical distribution), we performed a UPGMA classification based on the similarity index of Baroni-Urbani & Buser. The method of McCoy *et al.* [*Ecology* 67 (1986), 749] enabled us to detect the significant groups and to differentiate them from those groupings that could be generated at random. Logistic regression analyses and environmental gradient analyses (DCA and CCA) were performed in order to find the relationships between the environmental variables and the observed distributional patterns.

Results Sixteen chorotypes were obtained between the Cytiseae species of the Iberian Peninsula and the Balearic Islands. The thermal variables showed the greatest influence in species distribution. Specifically, temperatures (maximum, minimum and mean) of the coldest months were associated with the majority of the chorotypes.

Main conclusions The species of the Cytiseae tribe were not randomly distributed in space, and can be classified in groups of species with common distributional patterns. The importance of cold tolerance in the distribution of these species, as well as their preference for acidic soils, was demonstrated. Certain general tendencies seem to exist with respect to the distribution of the biota in the Iberian Peninsula, and these seem to be independent of the taxonomic groups involved and to be determined by convergent macroclimatic factors.

Keywords

Geographical distribution, classification, chorotypes, environmental variables, Iberian Peninsula, Balearic Islands.

RESUMEN

Objetivo Analizar cuantitativamente el patrón biogeográfico de las especies de la tribu Cytiseae Bercht. & J. Presl (= Genisteeae Benth.) en la Península Ibérica y las Islas Baleares e identificar los factores ambientales relacionados con el establecimiento de sus patrones de distribución.

Localización Península Ibérica e Islas Baleares, utilizando las 61 provincias administrativas como unidades geográficas operacionales.

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Métodos Para la identificación de corotipos se realizó una clasificación UPGMA, aplicando el índice de similitud de Baroni-Urbani & Buser. El método de McCoy *et al.* [*Ecology* 67 (1986) 749] nos permitió detectar aquellos grupos que resultaron ser significativos y diferenciarlos de aquellas agrupaciones que se pudiesen generar como producto del azar. Se llevaron a cabo análisis de regresión logística y de ordenación en gradientes ambientales (DCA y CCA), para encontrar la relación entre las variables ambientales y los patrones de distribución encontrados.

Resultados Se han obtenido 16 corotipos entre las especies de Cytiseae de la Península Ibérica y Baleares. Las variables térmicas han resultado ser las que en mayor medida están influenciando en la distribución de las especies. Concretamente, las temperaturas (máximas, mínimas y medias) del mes más frío son las que se asocian a la mayoría de los corotipos.

Conclusiones principales Las especies de la tribu Cytiseae no se distribuyen de forma azarosa en el espacio y pueden clasificarse en grupos de especies con un patrón de distribución común. Se comprueba la importancia de la tolerancia al frío en la distribución de estas especies y su preferencia hacia los suelos ácidos. Parece ser que existen ciertas tendencias generales en cuanto a la distribución de especies en la península, independientemente del grupo taxonómico y determinadas por factores macroclimáticos.

Palabras clave:

Distribución geográfica, clasificación, corotipos, variables ambientales, Península Ibérica, Islas Baleares.

INTRODUCTION

Among the main objectives of biogeography is the study of species distributional patterns, both spatially and temporally, and the determination of the underlying environmental factors related to these distributional patterns (Brown & Lomolino, 1998). If in nature there are groups of species that present common distributional patterns, then it should be possible to identify these group of species in concrete biogeographical units that can be classified and related to environmental variables (Real *et al.*, 1997).

The Iberian Peninsula and the Balearic Islands are of great biogeographical interest due to their great variety of climatic, lithologic and geomorphological contrasts that have repercussions for biota distribution (Domínguez *et al.*, 2000). These factors, combined with a palaeogeographical history of great activity, have generated a diverse and specialized flora (Sainz Ollero & Hernández Bermejo, 1981), principally Mediterranean, with temperate elements in the north and a few relics of the subtropical climate that existed until the ends of the Tertiary. However, even in the authentically Mediterranean taxonomic groups, there are morpho-functional characteristics that can only be explained by a tropical origin, while others have been acquired during the establishment of Mediterranean climatic conditions in the Quaternary (Herrera, 1992).

In general, the Iberian Peninsula is climatically characterized by a humidity gradient with high precipitation levels in the north-west and an increase of xeric conditions through the

south-east (Fernández-González, 1997). Lithologically, it is characterized by the dominance of acidic soils in the western half and basic soils in the eastern half of the Peninsula (Moreno Saiz *et al.*, 1998). Another characteristic with biogeographical implications in the Iberian Peninsula is the presence of apparent geographical barriers, such as the Straits of Gibraltar and the Pyrenees, which have created a relative isolation of the Peninsula with respect to the African continent and the rest of Europe (Vargas *et al.*, 1998). However, the isolating nature of these barriers is controversial and depends on the characteristics of the biological groups analysed.

The inclusion of the Balearic Islands in the phytogeographical studies of the Iberian Peninsula is relevant as they are continental islands that throughout their history maintained a strong relationship with the Peninsula, experiencing several contacts with the Levantine coast at the end of the Miocene. The high floristic similarity between Ibiza and the Peninsula demonstrate this fact (Moreno Saiz *et al.*, 1998).

The study of the flora of the Iberian Peninsula and Balearic Islands has made important progresses during the last few years, generating valuable information on the distribution of many taxa (Moreno Saiz *et al.*, 1998). For instance, several studies have analysed the geographical patterns of distribution of plant species in the Peninsula, making important advances in the phytogeographical knowledge of the area (e.g. Hernández Bermejo & Sainz Ollero, 1984; Morla & Pineda, 1985; Sainz Ollero & Hernández Bermejo, 1985; Moreno Saiz *et al.*, 1998; Ojeda *et al.*, 2000;

Márquez *et al.*, 2001). However, most of these studies have analysed the similarity in the floristic composition of different operational geographical unit (OGUs) in order to determine biogeographical units. A complementary approach is the study of the existence of particular distribution patterns that are shared by a group of species. If distribution patterns exist that are common to particular species, specific groups may be classified into biogeographical categories, which can be further analysed in order to assess the importance of different environmental factors involved in setting the patterns. For example, a study performed with the pteridophytes of the Iberian Peninsula (Márquez *et al.*, 1997), demonstrated that there were groups of species that share a geographical spatial distribution that was more similar than can be expected by chance alone, forming concrete groups called 'chorotypes'. Furthermore, the existence of several chorotypes was significantly related to environmental variables associated with water availability (precipitation and flooding), climatic stress and energy availability (temperature and solar light hours). Similar patterns could also be found and analysed in other taxonomic groups that have certain biogeographical importance (e.g. wide distribution and dominance in vegetation), taxonomic naturalness and high diversity (number of species). Understanding the geographical behaviour of some smaller groups could generate valuable biogeographical information for the Iberian Peninsula.

The Cytiseae Bercht. & J. Presl (= Genisteae Benth.) tribe (Leguminosae-Papilionoideae) generally includes shrubs that present clear adaptation syndromes to the Mediterranean climate (e.g. malacophilia and pubescence), which has given them a great diversification not only in the Peninsula, but also in the entire Mediterranean Basin and the Macaronesian Region (Talavera & Salgueiro, 1999). Some of the genera notably contribute to characteristic vegetation units within the Iberian Peninsula and Balearic Islands: the 'Retamales' of *Retama sphaerocarpa*, the 'Escobonales' dominated by *Cytisus*, the 'Tojales' of *Ulex* and *Stauracanthus*, and the 'Aulagares' of *Genista*, for example (Devesa Alcaraz, 1997). It is a group of great ecological importance, not only for its species diversity, but also for the capacity of these species to colonize a great variety of environments, including degraded forests and deforested areas (López González, 2001). Furthermore, the group constitutes a model system for the study of Mediterranean biogeographical patterns as they satisfy the requirements previously cited, and could generate useful information for the conservation of determined vegetation enclaves inside the Iberian Peninsula and the Balearic Islands.

In the present work, we analysed in quantitative form the distribution patterns of species of the Cytiseae tribe within the Peninsula and Balearic Islands, assuming that they are not randomly distributed in space and that they form concrete chorological groups in response to their environment. We identified the presence of significant species groups with a distribution more similar than expected by chance alone (cf. McCoy *et al.*, 1986; Vargas *et al.*, 1997), and detect the existence of environmental and/or geographical variables that can explain the observed geographical pattern of the species.

MATERIALS AND METHODS

Data collection

The administrative provinces of Spain and Portugal were used as OGUs (Crovello, 1981), consisting in a total of 61 provinces where the Balearic Islands Mallorca, Menorca and Ibiza are considered as independent OGUs (Fig. 1). This is an adequate type of OGU because they do not vary greatly in unit size and their number is sufficiently high to be able to detect natural patterns (Ojeda *et al.*, 1998; Márquez *et al.*, 2001).

Of the 400 species that constitute the Cytiseae tribe (Talavera & Salgueiro, 1999), the distribution of 109 species that were found inside the study area was determined using information on the presence of the species at each province. Such floristic information was obtained from the *Flora Ibérica* (Castroviejo *et al.*, 1999) because it provides well-documented and homogenous information. The naturalized or cultivated species were not included.

Temperature and precipitation data were obtained from one station per province from the National Institute of Meteorology (Instituto Nacional de Meteorología, INM) of Spain, the Meteorological Institute (Instituto Meteorológico, IM) of Portugal, and from Rivas-Martínez (1987). These data were also used to construct new variables that were indicators of environmental factors that could be related to species distributions. These were: mean annual temperature [Ta, from Rivas-Martínez, 1987 and Ta2 of INM (Spain) and IM (Portugal), information from two stations per province in this case], average maximum temperature of the coldest month (TMf), average minimum temperature of the coldest month (Tmf), average annual minimum temperature (Tma), average temperature of the coldest month (Tf), average temperature of the warmest month (Tc), negative thermic integral (Rivas-Martínez) (Itn), sum of the number of months with average monthly temperatures lower than 5 °C (S5°), average summer precipitation (Pv), two indices of humidity: Index of Lang (L)



Figure 1 Map of the Iberian Peninsula and Balearic Islands showing the geographical units used in the classification species analysis. See code of provinces in Appendix 1.

and Index of Philippi (Ph), Index of Mediterraneanity (RM) and of annual aridness (RA) of Rivas-Martínez, difference in the mean annual temperature for climatic stations within a province (ΔT), and the annual average amplitude of temperature (A_m). The only geographical variable considered was the altitude of each station (h) (see Fernández-González, 1997).

To replace the missing climatic information in some provinces, some climatic data were interpolated from known data using Kriging geostatistic method (Smith *et al.*, 1995). Concretely, in this way the data for the province of Ribatejo (Ta2, Tc, Tf and Tma) and the Beira Littoral (Tma) were obtained.

Analysis of species classification

Based on the presence-absence matrix of the 109 species in the 61 provinces, a cluster analysis was performed using the agglomerative algorithm UPGMA. The obtained groups were represented in a dendrogram. The index of Baroni-Urbani & Buser (1976) was used in the analysis to obtain the similarity value between each pair of species a and b of the matrix:

$$S^* = \frac{\sqrt{AD} + A}{\sqrt{AD} + A + B + C},$$

where A and B are the number of provinces where only the species a and b are present, respectively, C is the number of provinces where the species a and b are present simultaneously, and D is the number of provinces where neither a or b are present.

Using the methodology proposed by McCoy *et al.* (1986) and modified by Real *et al.* (1992b), to identify the groups of species that constituted chorotypes (see also Vargas *et al.*, 1997). For this, we transformed our similarity matrix into a matrix of signs of '+', '-' or '0', depending on whether the similarity value between the species is significantly higher than expected at random, significantly lower, or without any significant difference, respectively. This operation is based on a critical value (for $n = 61$; $P < 0.05$) proposed in Baroni-Urbani & Buser (1976). Subsequently, a submatrix of signs was built that only includes the species of the evaluated node, differentiating between three zones: zone A and zone B, where the zone corresponds to each group of species that the node separates, and the zone A \times B, corresponding to the intersection between the zones A and B. Observing the proportion of the different signs in the three zones, we obtained the parameters necessary to differentiate the groups that really have a biogeographical sense from those that are generated randomly by the analysis. The parameters DW (A \times A), DW (B \times B) provide an idea of how large the significant positive similarity (+) is in the zones A \times A or B \times B, but not in the zone A \times B. Definitively, these are indicators of the internal homogeneity of each group, a necessary (but not sufficient) condition for chorotype constitution. The parameter DS estimates if the significant negative similarity proportion (-) tends to concentrate in the zone A \times B, but not in A \times A or in B \times B, indicating the magnitude of the difference existing between both groups with respect to their geographical

distribution. An independence test (G -test) was performed to evaluate the statistical significance of each node, where the distribution of the signs +, - and 0 between the three zones is analysed to obtain the parameters GS and GW (see details in McCoy *et al.*, 1986). If GS is significant and DS $>$ 0, there is a strong segregation between the groups that separate the node, while if GW is significant and DW $>$ 0, the segregation is weak (McCoy *et al.*, 1986; Real *et al.*, 1992a; Vargas *et al.*, 1997).

Relation between chorotypes and environmental variables

Two types of analysis were performed to study the relations between the environmental variables and the pattern followed by the species groups: logistic regression analysis and indirect (DCA) and direct (CCA) gradient analysis.

The logistic regression equation was used to identify those environmental variables that significantly influenced the presence-absence of each chorotype. Comparing the values of the 'odd ratio' of the regression coefficients and selecting those with the highest value allowed the identification of those variables with the higher weight in the logistic model, and consequently, those associated to a greater extent with the presence of the chorotype.

While the indirect gradient analysis (DCA) provides information on the floristic relations between the chorotypes, the canonic correspondence analysis (CCA) orders these relationships across an environmental gradient. The values of both analyses were compared to determine if the environmental variables were sufficient to explain the floristic gradient found in the DCA. Analysing the magnitude and sign of the intraset correlations, we could establish the relative importance of each environmental variable in the distribution of the chorotypes (see ter Braak, 1986, 1987). For the ordination analyses, we included only the provinces that presented more than 50% of the species of the chorotype and those variables that were significant in the logistic regressions, eliminating those that generated multicollinearity. The objective was to obtain a more defined pattern, and in this way be able to detect more precisely the environmental relationships of the chorotypes (Vivanco, 1999).

RESULTS

Chorotypes

Figure 2 shows the dendrogram obtained with the UPGMA clustering of species according to their geographical similarity. Sixteen chorotypes of Cytiseae were found for the Iberian Peninsula and the Balearic Islands. Of the 109 studied species, only two did not show geographical similarity with the rest. These were *Genista dorycnifolia* FontQuer and *Adenocarpus desertorum* S. Castroviejo. The first is a Balearic endemic (Ibiza) and the second is only found in the rocky areas among brushwood established on the granite of Cáceres (López González, 2001). All the significant forks that segregate chorotypes were weak, except in the case of

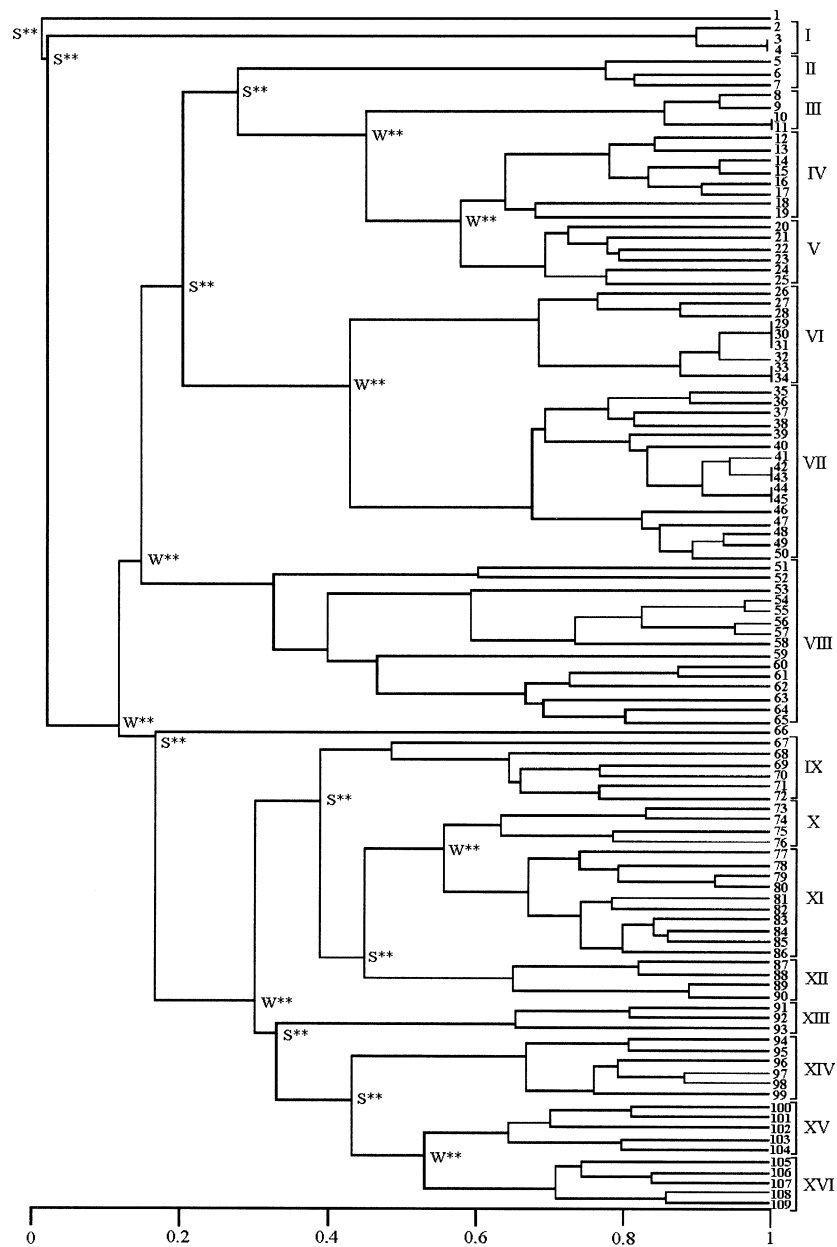


Figure 2 Resulting dendrogram of the 109 species classified in function of its geographical similarity. Chorotypes (roman numbers) and significant segregations are indicated (S: strong segregation, W: weak segregation, $*P < 0,05$, $**P < 0,01$). See code of species in Appendix 2.

chorotypes I, II, IX, XII, XIII and XIV which were strongly segregated from the rest (Table 1). These chorotypes are characterized because they contained few species and one or more endemics among them. Then, in this case, a weak or strong segregation could provide information about the floristic singularity of our chorotypes.

The maps indicating the geographical localization of the biotic elements obtained are shown in Fig. 3. The provinces are differentiated as a function of the percentage of species of the chorotype that they contain.

Chorotype I consisted of three species. One of them is endemic to the Mallorca Island (*Genista majorica* P.), whose

particular distribution could be the cause of the low similarity found with respect to the rest of chorotypes (Table 1, Fig. 3).

The chorotypes II and III were located in the midwest and the southern coast of Portugal, respectively (Fig. 3), characterized by abundance of limestone soils. Among these species were *Ulex densus* Welw. ex Webb (chorotype II) and *Ulex erinaceus* Welw. ex Webb (chorotype III), both basophilic endemisms.

The chorotypes IV, V, VI and VII showed the largest percentage of their species in the southern half of the Peninsula, all with the tendency to be found in provinces with oceanic influence (Fig. 3). The most frequent species of these choro-

Table 1 Significant segregation between groups of species at each node in the dendrogram. * $P < 0.05$, ** $P < 0.01$. See Materials and methods for the meaning of the obtained parameters

Group 1	Group 2	Coefficient	DW A × A	DW B × B	DS	GW	P	GS	P
1	2–109	0.012	-6.5×10^{-8}	-0.484	0.114	22.89	**	59.22	**
2–4	5–109	0.021	0.701	-0.478	0.108	54.42	**	114.19	**
5–65	66–109	0.117	-0.358	-0.272	-0.330	541.94	**	862.24	**
5–50	51–65	1.470	-0.140	0.033	-0.109	257.75	**	242.95	**
5–25	26–50	0.204	0.052	0.281	0.062	264.11	**	251.54	**
5–7	8–25	0.278	0.567	0.171	0.164	26.18	**	36.12	**
66	67–109	0.165	-1.6×10^{-7}	-0.232	0.212	16.53	**	29.59	**
67–90	91–109	0.301	0.019	-0.085	-0.073	168.88	**	113.92	**
91–93	94–109	0.331	0.663	0.095	0.271	26.00	**	24.38	**
94–99	100–109	0.432	0.465	0.223	0.100	24.60	**	18.32	**
67–72	73–90	0.39	0.307	0.166	0.105	43.61	**	21.31	**
73–86	87–90	0.45	0.305	0.538	0.116	30.47	**	25.98	**
26–34	35–50	0.429	0.333	0.295	-0.074	83.23	**	56.43	**
8–11	12–25	0.45	0.400	0.166	-0.042	12.08	**	25.98	**
12–19	20–25	0.579	0.274	0.363	-0.262	23.48	**	4.69	*
100–104	105–109	0.53	0.477	0.515	-0.037	28.26	**	4.44	*
73–76	77–86	0.556	0.344	0.340	-0.201	23.75	**	6.04	*

types (e.g. *Ulex australis* Clemente, *Genista hirsuta* Vahl, *Teline monspesulana* (L.) Koch and *Genista umbellata* (L'Hér.) Dum. Cours.) are usually found in sandy coasts with a warm temperate climate.

A large portion of the species of chorotype VIII are usually found on basic soils in cleared and sunny brushwood areas (e.g. *Genista scorpius* (L.) D.C.), coinciding its distribution with the predominantly limestone area of the Peninsula (Fig. 3).

Chorotype IX, located in the Sistema Central, and chorotype XII, located in Montes de León, (Fig. 3) are characterized by their dominance in species of mountainous brushwood such as *Genista cinerascens* Lange. and *Echinopartum ibericum* Rivas Mart., Sánchez Mata & Sancho.

The majority of the species of the chorotypes X and XI were found close to the Atlantic coast of the Peninsula (Fig. 3), where *Ulex europaeus* L. and *Cytisus striatus* Rothm. are representative species. These species grow in siliceous soils and require greater humidity.

Chorotypes XIII, XIV and XVI were the most septentrional, and their most characteristic species (*Cytisus decumbens* Spach, *Genista micrantha* Ortega and *Genista hispanica* L., respectively) can be found in grasslands and humid forests, such as beech or oak forests.

Finally, chorotype XV was characterized by a group of species of wide distribution inside the studied zone (i.e. *Cytisus scoparius* Link).

Logistic regressions

In general, the variables involving temperature were those with the greatest influence on chorotype distribution (Table 2). Table 3 shows the 'odds ratio' values of those variables with strongest relationships with chorotypes distribution. Particularly remarkable was the positive relationship found between TMf and chorotypes I, II, III and VI and the negative

relationship with chorotype XV. Another important thermic variable was the mean annual temperature (Ta and Ta2), which explained the presence of many of the chorotypes found (IV, V, VII, IX, X and XIII). Chorotypes XII and XIV showed a positive relationship with Tmf, while chorotype XI showed a relationship with the temperature range (ΔT). According to this analysis, only the presence of chorotype VIII was affected by altitude (h).

Ordination analyses

The first two axes obtained in the DCA analysis (based exclusively on floristic information) explained 26.3% of the variation found (Table 4). The province of Murcia was excluded from the analysis because it did not present 50% or more of the species from any chorotype. Similarly, the variables Ta and Tf were also eliminated as they generated multicollinearity.

The floristic ordination of the chorotypes is showed in Fig. 4. All chorotypes were ordered principally along axis 1, which corresponded to a latitudinal gradient from north to south, where the most septentrional chorotypes were located near the origin and those from the south in the right extreme of the graph. Although the gradient represented by axis 2 is narrower, and there is no clear trend in the ordering, the position of chorotypes VI and VII (located in the Andalusian coastal provinces) in the negative range of that axis is notable.

Table 4 includes as well the eigenvalues of the first two axes obtained in the CCA. In comparison with the eigenvalues obtained in the DCA, a small decrease in the values was observed. Furthermore, the relative position of chorotypes in both figures (DCA and CCA, Figs 4 & 5, respectively) was similar. All this indicates that the environmental variables included in the analysis were sufficient to explain the floristic variation found in the DCA.

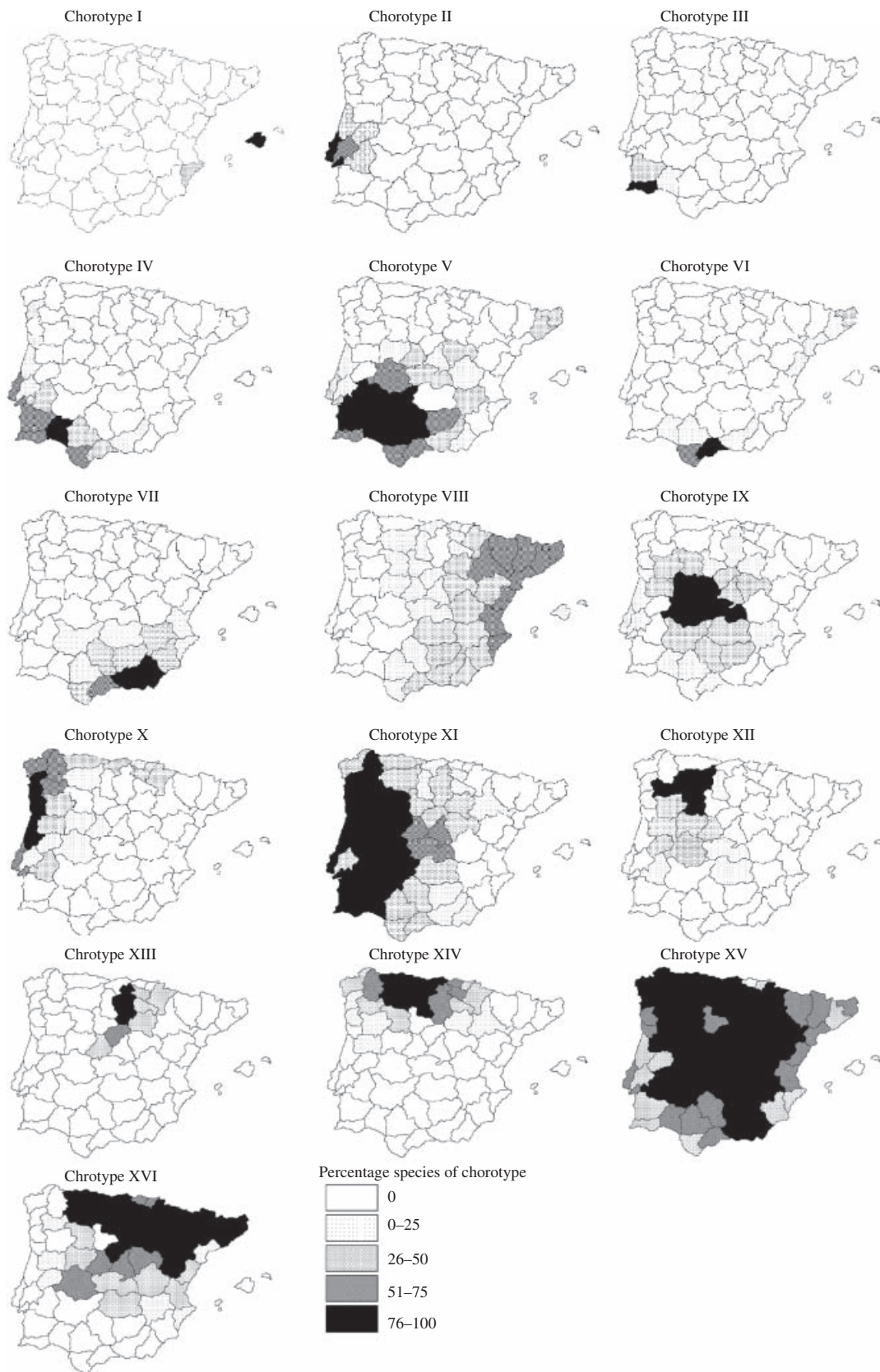


Figure 3 Distribution maps of the 16 chorotypes found for the Cytiseae tribe species in the Iberian Peninsula and Balearic Islands. Provinces have different colours depending on the percentage of species of the chorotype present.

Table 2 Logistic regressions showing the significant relations between environmental variables and the present-absence of each chorotype. Those variables with greater weight in the logistic model are indicated in bold. See codes of variables in Materials and Methods

Chorotype	P	Logistic model
I	0.0147	$Y = -21.52 + 12.07 \text{ Ta} + \mathbf{21.77 \text{ TMf}} - 2.80 \text{ Tf} - 4.14 \text{ L} - 21.48 \text{ Ta}_2$
II	0.0000	$Y = -332.94 - 8.93 \text{ Ta} + \mathbf{19.61 \text{ TMf}} + 12.90 \text{ Tmf} + 17.40 \text{ Am} - 86.42 \text{ RA}$
III	0.0336	$Y = -13.68 + \mathbf{0.70 \text{ TMf}} + 0.35 \text{ Tmf}$
IV	0.0000	$Y = 2.90 + 0.23 \text{ Ta} + 1.42 \text{ TMf} - 2.13 \text{ Tf} - 2.14 \text{ Tc} - 0.11 \text{ Pv} + \mathbf{2.96 \text{ Ta}_2} - 0.49 \Delta\text{T}$
V	0.0002	$Y = -3.39 + \mathbf{1.84 \text{ Ta}} - 0.30 \text{ TMf} - 0.61 \text{ Tmf} + 0.10 \text{ Tf} - 0.74 \text{ Tc} + 0.25 \text{ S5}^\circ - 1.84 \text{ Ph}$
VI	0.0036	$Y = -2.38 + 0.20 \text{ Ta} + \mathbf{0.21 \text{ TMf}} - 0.13 \text{ Tmf} - 0.23 \text{ Am} - 0.05 \text{ Pv}$
VII	0.0000	$Y = -49.75 + \mathbf{1.67 \text{ Ta}} + 0.64 \text{ TMf} - 1.27 \text{ Tmf} + 1.36 \text{ Tf} + 0.96 \text{ Am} - 0.56 \text{ Tma} - 0.97 \text{ RA}$
VIII	0.0005	$Y = -6.88 - 0.63 \text{ Tmf} + 0.59 \text{ Tf} + 0.30 \text{ Am} + \mathbf{0.71 \text{ h}}$
IX	0.0431	$Y = -1.34 - 0.39 \text{ Tf} - 0.24 \text{ Tc} - 0.04 \text{ Pv} + \mathbf{0.87 \text{ Ta}_2} - 0.26 \text{ Tma} + 0.59 \text{ S5}^\circ + 0.23 \Delta\text{T}$
X	0.0001	$Y = + 5.86 - 5.11 \text{ Tc} + 2.56 \text{ Am} + 0.02 \text{ Pv} + \mathbf{4.86 \text{ Ta}_2} + 0.59 \Delta\text{T}$
XI	0.0001	$Y = 8.47 - 0.29 \text{ TMf} - 0.25 \text{ Tmf} - 0.05 \text{ Pmv}_2 - 3.29 \text{ ETP/P} + 0.10 \text{ ETPv/Pv} + \mathbf{0.33 \Delta\text{T}}$
XII	0.0434	$Y = 5.53 - 0.50 \text{ TMf} + \mathbf{0.40 \text{ TMf}} - 0.23 \text{ Tf} + 0.01 \text{ Tc} - 0.04 \text{ Pv}$
XIII	0.0033	$Y = 4.05 + \mathbf{0.19 \text{ Ta}} - 0.00 \text{ TMf} - 1.45 \text{ Tf} + 0.04 \text{ Pv} - 3.27 \text{ h}$
XIV	0.0000	$Y = 24.92 - 0.20 \text{ Ta} - 1.63 \text{ TMf} + \mathbf{1.24 \text{ Tmf}} - 0.82 \text{ Tf} - 7.38 \text{ h} + 0.30 \text{ Itn}$
XV	0.0167	$Y = 25.68 - \mathbf{0.35 \text{ TMf}} - 1.36 \text{ Tmf} - 0.75 \text{ Am}$
XVI	0.0000	$Y = -6.23 - 2.47 \text{ Ta} - 0.91 \text{ TMf} + \mathbf{3.52 \text{ Tf}} + 1.11 \text{ Tc} + 1.22 \text{ Am} + 0.14 \text{ Pv} - 1.51 \text{ Ta}_2 + 1.98 \Delta\text{T}$

Table 3 'Odds ratio' values of those variables better correlated with the chorotypes distribution

Chorotype	Variable	Odds ratio
I	TMf	0.06
II	TMf	32.8×10^7
III	TMf	2.01
IV	Ta ₂	19.41
V	Ta	6.31
VI	TMf	21.93
VII	Ta	5.35
VIII	h	2.05
IX	Ta ₂	0.87
X	Ta ₂	129.74
XI	ΔT	1.39
XII	Tmf	1.49
XIII	Ta	1.21
XIV	Tmf	3.48
XV	TMf	0.70
XVI	Tf	33.75

Table 4 Eigenvalues and percentage of variance explained by the two first axes in the indirect gradient analysis (DCA) and direct gradient (CCA) analysis

Axes	Eigenvalues		Explained variance (%)	
	DCA	CCA	DCA	CCA
1	0.656	0.548	15.504	10.490
2	0.454	0.358	26.249	17.341

The chorotypes situated in the positive area of axis 1 of the CCA, were those that are distributed in the Northern peninsular half or in mountainous areas (VIII, IX, XII, XIII, XIV and XVI), as well as those that showed a wide distribution in the peninsula (XV) (Fig. 5). Humidity index

Table 5 Intraset correlations between environmental variables and the first two axes of the canonical correspondence analysis

Variable	Intraset correlations	
	Axis 1	Axis 2
TMf	-0.731	-0.233
Tmf	-0.760	-0.135
Tc	-0.526	0.012
Am	-0.074	0.233
Pv	0.751	0.155
h	0.431	0.373
Ta ₂	-0.690	-0.284
L	0.257	0.084
Itn	-0.208	-0.186
S5°	0.388	0.330
Ph	0.624	0.032
RA	-0.150	0.082
RM	-0.750	0.300
ΔT	-0.166	0.325

(Pv, Ph and L), and other variables such as h and S5°, were the environmental variables associated with the distribution of these chorotypes. Throughout the negative area of axis 1, we found the rest of the chorotypes, including those with an oceanic influence, as well as those located in the south and in the west of the peninsula, such as the Balearic chorotype. These chorotypes were correlated with thermic variables and the Mediterraneanity index. With respect to the ordering in axis 2, the position of chorotypes XIII and VII in the positive area is notable, and could be correlated with ΔT, h and S5°.

According to the intraset correlation values, axis 1 was principally and positively correlated with Pv and Ph, and negatively with TMf, Tmf, Ta₂, Tma and RM (Table 5). However, axis 2 showed a very low correlation with all the

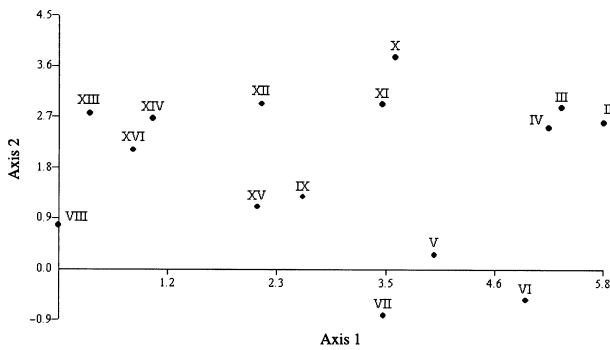


Figure 4 Detrended correspondence analysis (DCA) giving the floristic relations between chorotypes.

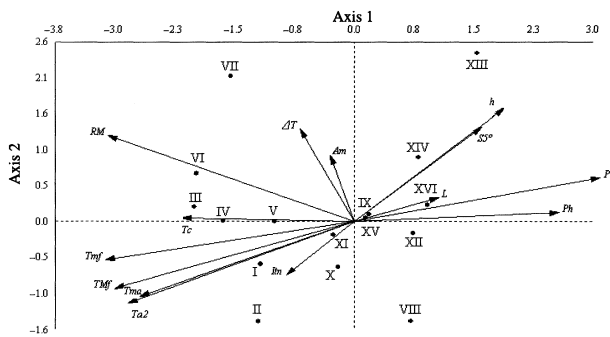


Figure 5 Canonical correspondence analyses (CCA) of chorotypes throughout a continuous environmental gradient. See codes of variables in Materials and Methods.

variables considered, the highest positive values being the correlation with $S5^\circ$ and h (Table 5).

DISCUSSION

Of the 109 species of Cytiseae in the Iberian Peninsula analysed, only two of them did not segregate to form part of any of the 16 chorotypes found. This was basically caused by the fact that these species did not present a significant geographical similarity with the rest of the species, which resulted in a strong segregation in the classification dendrogram. According to Real *et al.* (1992b), the species that do not constitute chorotypes are those that are distributed randomly and independently of the others, using space as a continuum, and being replaced by other species over time. However, in our case, both species (*Genista dorycnifolia* and *Adenocarpus desertorum*) are endemics with a very restricted distribution, which is not random, but rather a product of isolation due to geographical and/or ecological barriers (Costa, 1997).

The rest of the species of the tribe have been classified in reasonably discrete groups with a common distribution patterns, which indicates that they do not occupy space at random, suggesting floristic and/or ecological relationships between the species that constituted each chorotype. Furthermore, this suggests that such species could respond in the same way to the factors that determine their distribution.

Márquez *et al.* (1997) performed a biogeographical analysis with the pteridophytes of the Iberian Peninsula and found chorotypes with patterns very similar to those found in our study, despite the fact that they are very dissimilar taxonomic groups. For example in pteridophytes, chorotypes VI, VIII, X, XI and XIII coincide in distribution with our chorotypes X, XI, VIII, XV and XIV, respectively. This congruence between studies performed with different groups suggests the possibility that at this geographical scale, environmental factors cause similar distribution patterns in the biota.

Although by definition each chorotype is a set of species with a coincidence in their spatial distribution that is greater than expected at random, there were common trends in several chorotypes with respect to their geographical localization inside the Iberian Peninsula. We found chorotypes (IV, V, X and XI) that shared a distribution along the Atlantic Coast under an oceanic climate and over acid substrates, differing from other chorotypes that were located in areas with basic substrates and a Mediterranean environment (I and VIII). However, other chorophytes tend to be distributed towards the Cantabrian and Pyrenean slopes (XII, XIII, XIV and XVI), while others were located in the southern Peninsula (VI and VII). Similar trends were found in the endemic dicotyledons, despite the application of different grouping techniques in the study of Sainz Ollero & Hernández Bermejo (1985). These authors highlighted the floristic peculiarity of the Gaditan-Onuvo-Algarviense littoral, the Baetic Ranges, the Murcian-Almerian area and the Balearic Islands. More recently, Moreno Saiz *et al.* (1998) have also recognized the floristic peculiarity of these areas with the study of distributional patterns of endemic monocotyledons. The peculiarity of the above-mentioned areas is also demonstrated in our study of the Cytiseae tribe, in which, higher number of species were found forming chorotypes located in those same areas (see chorotypes I, III, IV, VI and VII).

Ojeda *et al.* (1998), also using administrative provinces as OGU, established floristic regions based on the distribution of the Ericaceae species of the Iberian Peninsula. Some of the floristic regions found there are also coincident with the areas of higher species richness in several of our chorotypes. Chorotypes IV, VI, VII, VIII and XI present a geographical localization similar to those regions (see Ojeda *et al.*, 1998). Therefore, although the concepts of biotic region and chorotype imply two different forms of classification, they are not completely disconnected as the patterns found in both cases could be responding to similar environmental factors.

In the south of the Iberian Peninsula, there were several chorotypes with a very restricted distribution (II, III, IV, VI and VII). These chorotypes are characterized by the higher number of endemic species included, and for the species with distribution areas extending to north-west Africa. This result could be related to the geological process that defined the history of the Strait of Gibraltar. Five million years ago, Europe separated from the African continent, resulting in an intense speciation and generation of many endemisms in southern Spain and northern Morocco (Valdés & Parra, 1999). It seems

that this area coincides with the centre of the highest diversity of the Cytiseae tribe around the world. Future research should analyse the historic and phylogenetic factors that have influenced the distribution of this tribe in the Iberian Peninsula, Balearic Islands and northern Morocco.

We found that in general, and at a wide scale, temperature was the factor most associated with the presence of chorotypes. Specifically, the maximum, minimum and average temperatures of the coldest month significantly correlated with the presence of 50% of the chorotypes, which indicates the importance of cold tolerance in the distribution of these species. As the correlation is positive, these chorotypes are most probably found in areas where winter is mild, with not very low freezing temperatures. This makes sense if we consider that these species have clear adaptations to high temperatures and strong solar radiation (e.g., pubescence, leaf reduction and presence of spines) being characteristic for the Mediterranean climate, which is the most common climate along the Iberian Peninsula (see Herrera, 1992). These conclusions are in agreement with the suggestions of Sakai & Weiser (1973), Sakai & Larcher (1987) and Jeffree & Jeffree (1994) who emphasized the importance of temperature in the distribution of woody species, particularly the lowest winter temperatures. Recently, Teneb *et al.* (2004) found that temperature, particularly the low temperature of winter, is the main environmental factor involved in the distribution patterns of the woody flora of south-central Chile. This zone of central Chile presents strong climatic equivalencies with the Iberian Peninsula, with a prevalence of the Mediterranean-type climate in most of the region and the presence of a transitional zone to a more humid temperate climate.

When we analysed the relationship between chorotypes and environmental variables in the CCA, the importance of variables involving temperature was also observed. Chorotypes from the South (I–VII) were associated with locations characterized by high temperatures and with a truly Mediterranean climate. Chorotypes from the north (XII, XIII, XIV and XVI) showed a greater tolerance to lower temperatures and seems to require higher precipitation that is more evenly distributed throughout the year (climate typical of the Euro-Siberian region). The rest of the chorotypes (VIII, IX, X, XI and XV) showed intermediate characteristics to the types previously described. In the biogeographical study of the Mediterranean heath species of Ojeda *et al.* (1998), the thermal variables (average minimum and mean annual temperatures) were significant in the multiple regression analysis, rejecting the variables related to precipitation as determining factors in their distribution. However, for fern species (Márquez *et al.*, 1997), water availability was the factor that best explained the presence of chorotypes, obviously due to the importance of this resource in the life cycle of the pteridophytes (Salvo, 1997).

Although not evaluated in our study, when observing the distribution of geological substrates in the Peninsula and the geographical location of the chorotypes, the soil type appears to be an important factor (see Lobo *et al.*, 2001). For example,

it is more probable to find acidophyllous species in the chorotypes of the western peninsula and basophyllous species in the east. Indeed, the Cytiseae species are generally found in the acidic zone of the western Peninsula, with exceptions, frequently sharing communities with the heath species (Rivas-Martínez, 1979), as can be seen in our results with a large number of chorotypes localized in the west half of the Peninsula (IV, V, IX, X, XI, XII and XIV).

Our results suggest that there are certain general tendencies with respect to species distribution in the Iberian Peninsula. Interestingly, these tendencies are independent from the taxonomic group analysed (e.g. Márquez *et al.*, 1997, 2001; Vargas *et al.*, 1998), and seem to be determined by convergent macroclimatic factors. Only the use of exhaustive numerical techniques applied to different taxa, and accompanied with probabilistic methods as used here, can shed more light on the presence and persistence of the complex biographical patterns found in the Iberian Peninsula.

ACKNOWLEDGMENTS

We would like to thank Olivia Infante and María Ángeles González for their participation in data collection and David Páez and Alejandra Jiménez for their assistance with the maps. Research funded by P02-051-F ICM.

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Appendix 1 Code of administrative provinces of Spain and Portugal

Code	Administrative provinces
Spain	
A	Alicante
Ab	Albacete
Al	Almería
Av	Ávila
B	Barcelona
Ba	Badajoz
Bi	Vizcaya
Bu	Burgos
C	La Coruña (A Coruña)
Ca	Cádiz
Cc	Cáceres
Co	Córdoba
CR	Ciudad Real
Cs	Castellón
Cu	Cuenca
Ge	Gerona
Gr	Granada
Gu	Guadalajara
H	Huelva
Hu	Huesca
J	Jaén
L	Lérida (Lleida)
Le	León
Lo	Logroño
Lu	Lugo
M	Madrid
Ma	Málaga
Mu	Murcia
Na	Navarra
O	Asturias (Oviedo)
Or	Orense (Ourense)
P	Palencia
PM	Islas Baleares
Mll	Mallorca
Mn	Menorca
Ib	Ibiza
Po	Pontevedra
S	Cantabria (Santander)

Appendix 1 *continued*

Code	Administrative provinces
Sa	Salamanca
Se	Sevilla
Sg	Segovia
So	Soria
SS	San Sebastián (Guipúzcoa)
T	Tarragona
Te	Teruel
To	Toledo
V	Valencia
Va	Valladolid
Vi	Álava (Vitoria)
Z	Zaragoza
Za	Zamora
Portugal	
AAI	Alto Alentejo
Ag	Algarve
BA	Beira Alta
BAl	Baixo Alentejo
BB	Beira Baixa
BL	Beira Litoral
DL	Douro Litoral
E	Extremadura
Mi	Minho
R	Ribatejo
TM	Tras-os-Montes (Alto Douro)

Appendix 2 Code of species. Nomenclature according to Castroviejo *et al.* (1999)

Code	Species
1	<i>Genista dorycnifolia</i> Font Quer
Chorotype I	
2	<i>Genista tricuspidata</i> Desf.
3	<i>Genista valdés-bermejoi</i> Talavera & L. Sáez
4	<i>Genista majorica</i> Cantó & M.J. Sánchez
Chorotype II	
5	<i>Ulex airensis</i> Espírito Santo & al.
6	<i>Ulex jussiaei</i> Webb
7	<i>Ulex densus</i> Welw. ex Webb

Appendix 2 *continued*

Code	Species
Chorotype III	
8	<i>Stauracanthus spectabilis</i> Webb
9	<i>Ulex argenteus</i> Welw. ex Webb
10	<i>Ulex erinaceus</i> Welw. ex Webb
11	<i>Adenocarpus anisochilus</i> Boiss.
Chorotype IV	
12	<i>Lupinus cosentinii</i> Guss.
13	<i>Calicotome villosa</i> (Poir.) Link
14	<i>Stauracanthus genistoide</i> (Brot.) Samp.
15	<i>Ulex australis</i> Clemente
16	<i>Stauracanthus boivinii</i> (Webb) Samp.
17	<i>Retama monosperma</i> (L.) Boiss.
18	<i>Adenocarpus gibbsianus</i> Castrov. & Talavera
19	<i>Genista ancistrocarpa</i> Spach
Chorotype V	
20	<i>Cytisus arboreus</i> (Desf.) DC.
21	<i>Adenocarpus telonensis</i> (Loisel.) DC
22	<i>Lupinus micranthus</i> Guss.
23	<i>Genista hirsuta</i> Vahl
24	<i>Ulex eriocladus</i> C. Vicioso
25	<i>Genista polyanthos</i> R. Roem. ex Willk.
Chorotype VI	
26	<i>Cytisus villosus</i> Pourr.
27	<i>Teline linifolia</i> (L.) Webb
28	<i>Teline monspessulana</i> (L.) K. Koch
29	<i>Ulex borgiae</i> Rivas Mart.
30	<i>Ulex baeticus</i> Boiss.
31	<i>Teline tribracteolata</i> (Webb) Talavera & P. E. Gibbs
32	<i>Genista tridens</i> (Cav.) DC.
33	<i>Echinospartum albigicum</i> Talavera & Aparicio
34	<i>Genista haenseleri</i> Boiss.
Chorotype VII	
35	<i>Calicotome intermedia</i> C. Presl
36	<i>Genista spartioides</i> Spach
37	<i>Ulex canescens</i> Lange
38	<i>Genista jimenezii</i> Pau
39	<i>Genista pseudopilosa</i> Coss.
40	<i>Chamaespartium undulatum</i> (Ern) Talavera & L. Sáez
41	<i>Adenocarpus decorticans</i> Boiss.
42	<i>Cytisus malacitanus</i> Boiss.
43	<i>Genista ramosissima</i> (Desf.) Poir.
44	<i>Cytisus galianoii</i> Talavera & P. E. Gibbs
45	<i>Genista versicolor</i> Boiss.
46	<i>Echinospartum boissieri</i> (Spach) Rothm.
47	<i>Genista umbellata</i> (L'Hér.) Dum. Cours.
48	<i>Spartium junceum</i> L.
49	<i>Genista cinerea</i> (Vill.) DC.
50	<i>Genista longipes</i> Pau
Chorotype VIII	
51	<i>Calicotome infesta</i> (C. Presl) Guss.
52	<i>Calicotome spinosa</i> (L.) Link
53	<i>Chamaespartium delphinense</i> (Verl.) Soják
54	<i>Cytosothillus sessilifolium</i> (L.) O. Lang
55	<i>Cytisus lotoides</i> Pourr.
56	<i>Echinospartum horridum</i> (Vahl) Rothm.
57	<i>Genista teretifolia</i> Willk.
58	<i>Genista ausetana</i> (O. Bolòs & Vigo) Talavera
59	<i>Genista valentina</i> (Willd. Ex Spreng) Steud.

Appendix 2 *continued*

Code	Species
60	<i>Ulex parviflorus</i> Pourr.
61	<i>Cytisus fontanesii</i> Spach, in sched.
62	<i>Teline patens</i> (DC) Talavera & P. E. Gibbs
63	<i>Genista pumila</i> (Debeaux & E. Rév. ex Hervier) Vierh.
64	<i>Erinacea anthyllis</i> Link
65	<i>Genista scorpius</i> (L.) DC.
66	<i>Adenocarpus desertorum</i> Castrov.
Chorotype IX	
67	<i>Echinospartum barnadesii</i> (Graells) Rothm.
68	<i>Lupinus hispanicus</i> Boiss. & Reut.
69	<i>Adenocarpus argyrophyllus</i> (Rivas Goday) Caball.
70	<i>Genista tournefortii</i> Spach
71	<i>Adenocarpus aureus</i> (Cav.) Pau
72	<i>Genista cinerascens</i> Lange
Chorotype X	
73	<i>Ulex europaeus</i> L.
74	<i>Adenocarpus lainzii</i> (Castrov.) Castrov.
75	<i>Ulex micranthus</i> Lange
76	<i>Genista berberidea</i> Lange
Chorotype XI	
77	<i>Cytisus grandiflorus</i> (Brot.) DC.
78	<i>Ulex minor</i> Roth
79	<i>Lupinus luteus</i> L.
80	<i>Genista triacanthos</i> Brot.
81	<i>Adenocarpus complicatus</i> (L.) J. Gay, in sched.
82	<i>Pterospartum tridentatum</i> (L.) Willk.
83	<i>Lupinus gredensis</i> Gand.
84	<i>Cytisus multiflorus</i> (L'Hér.) Sweet
85	<i>Cytisus striatus</i> (Hill) Rothm.
86	<i>Genista falcata</i> Brot.
Chorotype XII	
87	<i>Echinospartum ibericum</i> Rivas Mart., Sánchez Mata & Sancho
88	<i>Genista hystrix</i> Lange
89	<i>Genista sanabrensis</i> Valdés Berm., Castrov. & Casaseca
90	<i>Genista carpetana</i> Lange
Chorotype XIII	
91	<i>Adenocarpus hispanicus</i> (Lam.) DC
92	<i>Cytisus decumbens</i> (Durande) Spach
93	<i>Genista pulchella</i> Vis.
Chorotype XIV	
94	<i>Genista micrantha</i> Gómez Ortega
95	<i>Genista obtusiramea</i> J. Gay ex Spach
96	<i>Cytisus commutatus</i> (Willk.) Briq.
97	<i>Ulex gallii</i> Planch.
98	<i>Cytisus cantabricus</i> (willk.) Rchb. Fil. & Beck
99	<i>Genista legionensis</i> (Pau) M. Lánz
Chorotype XV	
100	<i>Lupinus angustifolius</i> L.
101	<i>Cytisus scoparius</i> (L.) Link
102	<i>Retama sphaerocarpa</i> (L.) Boiss.
103	<i>Genista anglica</i> L.
104	<i>Genista florida</i> L.
Chorotype XVI	
105	<i>Cytisus oromediterraneus</i> Rivas Mart. & al.
106	<i>Chamaespartium sagittale</i> (L.) P. E. Gibbs
107	<i>Genista pilosa</i> L.
108	<i>Genista hispanica</i> L.
109	<i>Genista tinctoria</i> L.