

A biogeographical analysis of the European Atlantic lowland heathlands

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Abstract

Questions: What is the climatic envelope of European Atlantic heathlands and the relationship between their floristic geographical variability and climatic parameters? Are the biogeographic patterns extracted from genuine heath plants comparable to those extracted from the accompanying flora? To what extent does the species composition extracted from phytosociological data support the current theory of refuge areas of heath vegetation in southern Atlantic Europe during the Pleistocene ice ages?

Location: Atlantic Europe and NW Morocco.

Methods: The geographical territory in which Atlantic heathlands occur was divided into 23 sectors following geographic and chorological criteria. A presence–absence table with 333 taxa was then constructed with the available phytosociological data. The taxa were classified into different groups according to their phytosociological affinity. Several types of numerical analysis were performed with this matrix and the climatic data obtained from meteorological sources.

Results: Heathlands require a humid and oceanic climate and are limited by cold temperatures in the north and by summer droughts in the south. The highest floristic richness of this vegetation type is found in NW Iberia. Ordinations indicate a strong correlation between floristic composition of biogeographic sector and summer drought (Ios) and thermicity (It).

Conclusions: The main climatic factors determining lowland heathland floristic distribution are thermicity and summer drought. The current optimal conditions for heath flora in NW Iberia suggest that there were southern refuges during the Pleistocene ice ages from which northward expansion has taken place.

Keywords: Climatic variables; Detrended correspondence analysis; Lowland heathlands; Phytosociological data; Vegetation biogeography.

Abbreviation: DCA = detrended correspondence analysis.

Introduction

An essential aim of biogeography is to elucidate the distribution of organisms over the surface of the Earth in modern times and in the past (Brown & Lomolino 1998). Thus, the aim is to find general trends in the modern distribution of taxa in order to establish patterns that can be related to the history of geographical events in the past, such as climatic changes and variations in the geomorphology and relief of the land, in order to understand the processes that have driven distribution from the past to the present.

The Atlantic coasts of Europe advanced and retreated dramatically several times during the Pleistocene due to the recurrent cold–warm cycles (Lang 1994; Ehlers & Gibbard 2003). As a result, the Atlantic heathlands show, with particular clarity, hallmarks of the history of change in vegetation and climate that occurred across the continent during that period (Mitchell & Watts 1970; Coxon & Waldren 1995). Since the Pliocene, apart from temperature and precipitation changes, this vegetation suffered fluctuations in sea level and consequent changes in the coastline caused by the Pleistocene glaciations. Large areas that had been sea-free during cold maxima were flooded in warm periods, as they are now in the Holocene. Associated repeated migrations, extinctions and recolonizations occurred during Quaternary climatic changes, and the modern distribution of vegetation types and their constituent flora largely reflect this history. In relation to this, certain of the common species in this vegetation, such as *Calluna vulgaris*, exceed the range of this vegetation type and seem to have had northern refuges during ice ages (Bhagwat & Willis 2008). However, genetic studies on populations of this heather show that genetic variability is lower in northern populations than in southern ones (Mahy et al. 1997, 1999), demonstrating that in spite of successful Holocene expansion, western *Calluna* populations have experienced relatively similar episodes to the rest of the Atlantic European heathers.

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In present times, the other species that constitute this vegetation type are mainly distributed in Atlantic zones.

Atlantic heathland vegetation has attracted the attention of many researchers (Benito Cebrián 1948; Rivas-Martínez 1979; Ojeda et al. 1998). After a long period of field survey and intense analytical work, throughout the 20th century, phytosociologists have provided a large amount of data on most vegetation types of the European continent. These data can be exploited in many ways, and we have attempted to use them to perform biogeographic analysis, in a similar way to that carried out in a previous study of the Iberian Peninsula (Loidi et al. 2007). Heathlands are among the best surveyed vegetation types (Tüxen 1937; Braun-Blanquet & Tüxen 1952; Géhu 1975a; Oberdorfer 1978; Rivas-Martínez 1979; Fernández Prieto & Loidi 1984; Rodwell 1991; Dierßen 1996; Schaminée et al. 1996; Loidi et al. 1997; Botineau & Géhu 2005), and a relevant biogeographical survey using heath species was carried out by Ojeda et al. (1998) using a similar approach to that of the present survey; however, our method differs in that we use plant community data contained in phytosociological relevés.

Lowland heathlands form a morphologically well-defined vegetation type unique to the Atlantic coastal territories of Europe. This shrubby vegetation is dominated by heathers (*Calluna*, *Erica* and other Ericaceae), woody legumes, such as gorse (*Ulex*) and *Genista* species (Gómez-González et al. 2004), grasses and some other plants. The concept of heathland considered here is more restrictive than that used by authors such as Gorissen (2004), who includes all the European shrublands dominated by heathers, with neither floristic nor climatic restrictions. Note that at the other extreme, there is an even more restricted concept (Gimingham 1972), which only considers as heathland types of vegetation from the Atlantic zones of Europe that have a temperate climate and a strong oceanic character, excluding any Mediterranean features; hence, it excludes the heathlands that can be found in the Iberian Atlantic areas and those from inland territories of Western Europe.

Syntaxonomically, we have restricted the heathlands to the *Calluno-Ulicetea* class, and excluded the types that could be related to *Vaccinio-Piceetea* or *Cisto-Lavanduletea*, in the same way as Rivas-Martínez (1979) and Díaz González (1998). Overall, for the European continent, there is a large amount of data available in the form of relevés (Schaminée et al. 2007). These provide accurate and extensive information concerning the modern floristic composition of

heath communities along the Atlantic façade of Europe, to which a small district in northern Morocco has to be added due to its climatic and soil conditions (Deil 1984; Quézel et al. 1988). The surveyed area includes most of the Atlantic territories of Europe (Fig. 1). In Scandinavia, cold temperatures limit heathland distribution and smaller areas are involved, such as southern Sweden and the coastal fringe of western Norway. In the south, i.e. the Iberian Peninsula and N Morocco, summer drought, characteristic of the Mediterranean climate, severely restricts heathland to mountains with orographic rains or to exceptionally wet areas.

Heaths have been mainly used by man for compost or for grazing, and have been artificially expanded by humans all over Atlantic Europe (Gimingham 1972). This expansion has been linked to livestock breeding activity, with extensive use of fire since Neolithic times. In spite of the fact that most of the current European heathlands have a secondary, man-induced origin, there are some basic natural conditions associated with this vegetation: a climate with high rainfall and a strong oceanic nature, together with acidic substrata.

The purpose of this work is to analyse the actual floristic composition of the heath communities, and to relate it to climatic conditions in order to extract biogeographical conclusions. This procedure is supported by the assertion that the combination of plant species in communities provides information about the ecological conditions needed to support them, and thereby it is possible to reach some conclusions about their origin and history (Mejías et al. 2007).

This survey was planned as a trial to investigate the potential of the information contained in phytosociological data, which is very abundant in some areas of the world, to be exploited for biogeographic purposes. We use the European Atlantic heathlands as a case study and asked the following questions: What are the relationships between floristic composition and climatic conditions across the heathland areas in Europe? Are the biogeographical patterns extracted from genuine heath plants comparable to those extracted from the accompanying flora? Are there any indications for the existence of refuge areas of heath vegetation in Atlantic Europe during Pleistocene ice ages?

Methods

The geographic approach

The lowland heath vegetation included in the *Calluno-Ulicetea* class mostly occurs in the Atlantic

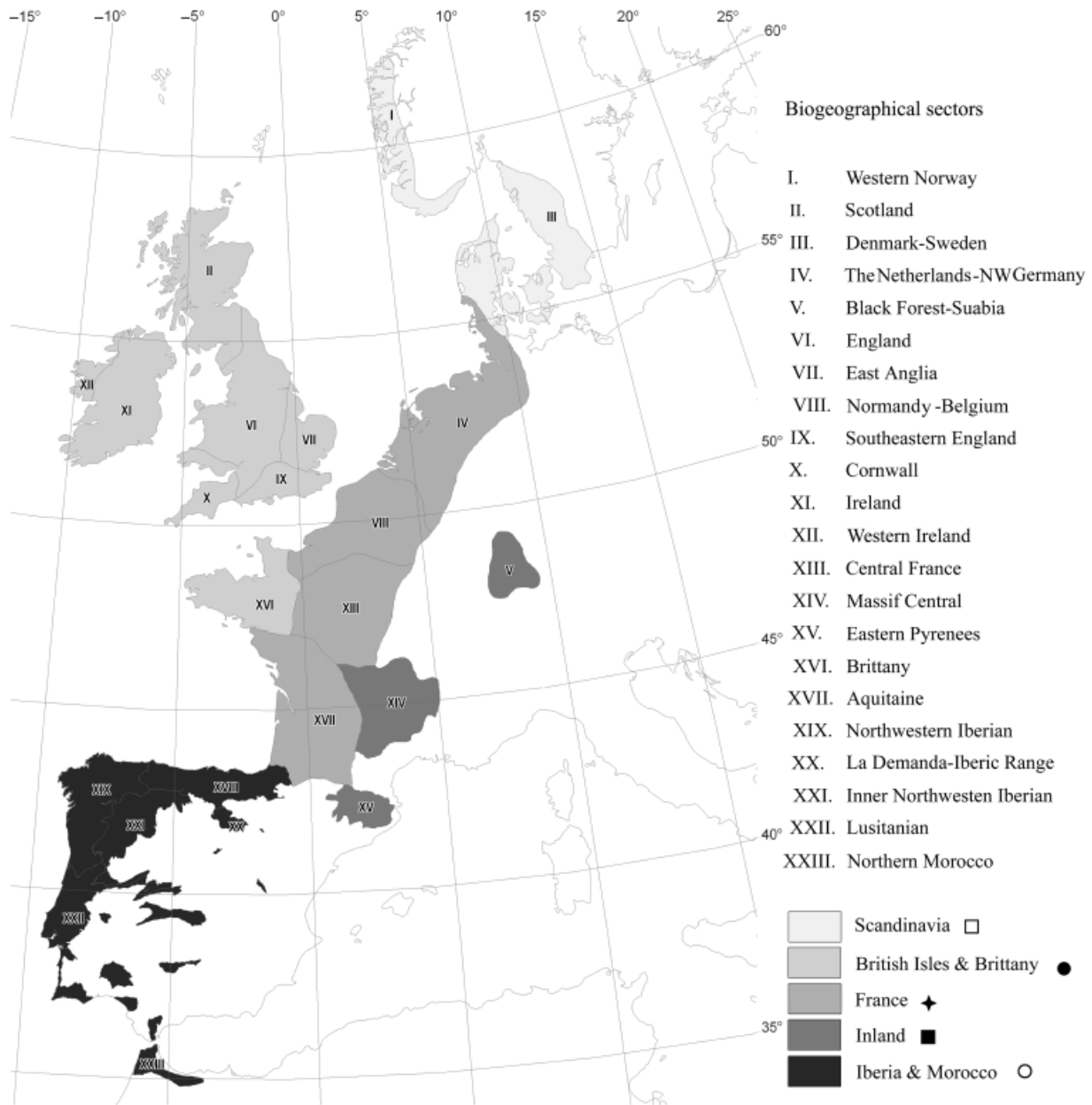


Fig. 1. Map of the area in which lowland heathlands occur in Europe and northern Morocco. The total area is divided into 23 sectors, numbered with Roman numerals, which are classified into five groups. Each group is identified with a symbol that is used in the ordination diagrams.

territories of the European continent, to which a small area in northern Morocco has to be added, as noted in the phytosociological literature. To survey the biogeographic diversity within this vast territory, it was divided *a priori* into 23 sectors of relatively comparable size (Fig. 1). These sectors were expected to express the biogeographic diversity. Several criteria were used to achieve this sectorization: geographic criteria such as insularity, geographical barriers, etc., and chorological criteria,

which have been applied to most of the area and which follow the distribution of certain significant taxa (heathers, gorses, etc.).

Constructing the floristic matrix

A presence-absence list of vascular plant taxa that occur in *Calluno-Ulicetea* communities was drawn up for each sector, and a basic matrix with 333 taxa to be used in the numerical analysis was

Table 1. Number of species in each ecological group in the 23 sectors into which the whole territory was divided.

| Sector | I | II | III | IV | V | VI | VII | VIII | IX | X | XI | XII | XIII | XIV | XV | XVI | XVII | XVIII | XIX | XX | XXI | XXII | XXIII |
|---|----|----|-----|----|----|----|-----|------|----|----|----|-----|------|-----|----|-----|------|-------|-----|-----|-----|------|-------|
| <i>Calluno-Ulicetea</i> | 2 | 7 | 4 | 6 | 4 | 8 | 5 | 10 | 11 | 13 | 8 | 10 | 14 | 8 | 10 | 20 | 16 | 40 | 51 | 24 | 39 | 49 | 16 |
| Orophilous and boreal | 5 | 8 | 6 | 9 | 5 | 3 | 0 | 2 | 1 | 0 | 3 | 3 | 1 | 5 | 6 | 1 | 0 | 6 | 3 | 3 | 4 | 1 | 0 |
| <i>Nardetea</i> | 3 | 12 | 3 | 13 | 13 | 14 | 2 | 11 | 6 | 14 | 9 | 11 | 10 | 11 | 10 | 12 | 10 | 19 | 16 | 12 | 14 | 6 | 1 |
| <i>Quercu-Fagetea</i> | 3 | 6 | 2 | 11 | 5 | 5 | 1 | 13 | 4 | 4 | 7 | 8 | 16 | 6 | 9 | 12 | 10 | 24 | 17 | 13 | 10 | 8 | 1 |
| <i>Molinio-Arrhenatheretea</i> | 1 | 7 | 1 | 6 | 5 | 7 | 1 | 6 | 2 | 8 | 5 | 7 | 9 | 6 | 7 | 9 | 6 | 11 | 11 | 9 | 10 | 8 | 3 |
| <i>Festuco-Brometea</i> and basiphilous | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 13 | 2 | 1 | 17 | 9 | 12 | 6 | 11 | 1 |
| <i>Quercetea ilicis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 6 | 1 | 3 | 14 | 14 | 2 | 7 | 36 | 20 |
| <i>Cisto-Lavanduletea</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 6 | 4 | 8 | 10 | 30 | 10 |
| <i>Cytisetea</i> | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 7 | 6 | 4 | 6 | 11 | 3 |
| Others | 1 | 5 | 2 | 7 | 4 | 4 | 1 | 8 | 0 | 5 | 1 | 9 | 8 | 3 | 7 | 16 | 6 | 47 | 46 | 22 | 22 | 45 | 14 |
| Total | 15 | 46 | 18 | 54 | 38 | 42 | 10 | 53 | 24 | 45 | 33 | 49 | 60 | 41 | 72 | 74 | 52 | 191 | 177 | 109 | 128 | 205 | 69 |

formed on the basis of these lists. Table 1 summarizes this matrix, where the species are classified into ecological groups. The source of information used was phytosociological literature available (both relevés and synoptic tables) for each of the territories. In order to standardize the data, bryophytes and lichens were removed because they are absent in data from the southern territories, and nitrophilous and ruderal species were also removed as they are present in only one sector. For the Iberian Peninsula and northern Morocco, information was taken from a previous study (Loidi et al. 2007), and for the rest of the study area, various phytosociological sources were used (see Appendix S1). The phytosociological tables from different associations of *Calluno-Ulicetea* class were synthesized to form one column for each sector. Other species were classified into ecological groups, defined by their phytosociological affinity (Oberdorfer 2001; Rivas-Martínez et al. 2002), and named as follows: *Calluno-Ulicetea* (genuine heathland species), *Quercu-Fagetea*, *Quercetea ilicis*, *Nardetea*, *Cisto-Lavanduletea*, *Cytisetea*, *Molinio-Arrhenatheretea*, *Festuco-Brometea*, basiphilous (species from basiphilous grasslands and scrublands) and orophilous and boreal. The rest of the species are included in a set of unclassified plants (others) with broad ecological requirements and a low indicator value, but that frequently appear in relevés.

The species richness in each sector is not correlated with sector size ($r = 0.108$) but shows a small positive correlation with the number of relevés used ($r = 0.59$; $P < 0.01$). However, species richness is more highly correlated with the number of associations (asoc) ($r = 0.62$; $P < 0.01$) and thus we used the

latter in the analysis as an indicator of habitat heterogeneity in each sector.

Climatic data

We compiled climatic data for the surveyed area using the WorldClim data set (Hijmans et al. 2005). For each sector we calculated various indexes and parameters from the available data: Pa (yearly average precipitation) and two bioclimatic indexes (Rivas-Martínez 2007): Ios (ombrothermic index for the 3 summer months; $(Pp/Tp) \times 10$), It (thermicity index; $(T+M+m) \times 10$) (T : yearly average temperature, M : average maximum temperature of the coldest month of the year, m : average minimum temperature of the coldest month of the year) and Ic (continentality index; $T_{\max} - T_{\min}$) (T_{\max} : average temperature of the warmest month; T_{\min} : average temperature of the coldest month) (Table 2).

Numerical analysis

Detrended correspondence analysis (DCA) was performed with CANOCO 4.5 (Microcomputer Power, Ithaca, US) to show relationship between the species composition of different sectors and the climatic indexes, topographic heterogeneity expressed by the altitude standard deviation (altSD) and habitat heterogeneity expressed by the number of associations (asoc). In order to determine whether *Calluno-Ulicetea* taxa had more weight in the ordination than species of the other types of ecological groups, several DCAs were carried out using different groups of species: (1) all species of the matrix, (2) only *Calluno-Ulicetea* species and (3) characteristic species of all ecological groups except those of *Calluno-Ulicetea*.

Results

Floristic data

Table 1 summarizes the basic data matrix and distribution of the existing flora in lowland heathlands in Europe. The proportion of species belonging to each of the different ecological groups in relation to *Calluno-Ulicetea* taxa present in each sector is represented in Fig. 2. The weight of the *Quercus-Fagetea* and *Nardetea* taxa decreases southwards, becoming almost insignificant in the Lusitanian and Moroccan sectors, while the Orophilous and boreal taxa are better represented in the northern sectors. In contrast, species of *Cytisetea*, *Quercetea ilicis*, *Cisto-Lavanduletea* and *Festuco-Brometea* and the basiphilous groups form part of the heathlands in the Iberian as well as in the French sectors, although to a lesser extent in the latter. In the Moroccan sector a large proportion of taxa are from the *Quercetea ilicis* and *Cisto-*

Table 2. Several bioclimatic parameters for the 23 sectors used in the analysis. asoc (number of associations), alt (mean altitude), altSD (altitude standard deviation) Pa (annual average precipitation), and two bioclimatic indexes (Rivas-Martínez 2007): Ios (ombrothermic index for the summer; $(Pp/Tp)^*10$ for the 3 summer months), It (thermicity index; $(T+M+m)\times 10$) (T : annual average temperature, M : average maximum temperature of the coldest month of the year, m : average minimum temperature of the coldest month of the year) and Ic (continentality index; $T_{max} - T_{min}$) (T_{max} : average temperature of the warmest month; T_{min} : average temperature of the coldest month).

| Sector | asoc | alt | altSD | Pa | Ic | Ios | It |
|--------|------|--------|-------|--------|------|------|-------|
| I | 1 | 440.4 | 329.6 | 2039.0 | 13.4 | 12.2 | 22.2 |
| II | 3 | 244.8 | 183.6 | 1221.0 | 11.8 | 6.6 | 104.5 |
| III | 3 | 72.4 | 45.6 | 737.6 | 17.1 | 4.4 | 53.5 |
| IV | 6 | 54.1 | 105.2 | 798.6 | 15.6 | 4.7 | 114.1 |
| V | 4 | 492.3 | 272.8 | 904.4 | 18.0 | 5.7 | 82.1 |
| VI | 4 | 152.2 | 128.5 | 860.7 | 12.7 | 4.5 | 143.8 |
| VII | 2 | 42.5 | 37.2 | 594.9 | 13.8 | 3.2 | 156.2 |
| VIII | 7 | 117.7 | 78 | 722.9 | 14.8 | 3.7 | 148.6 |
| IX | 3 | 75.5 | 51.7 | 726.0 | 13.4 | 3.2 | 168.5 |
| X | 5 | 138.2 | 105.9 | 1049.8 | 12.2 | 4.5 | 174.6 |
| XI | 1 | 111.9 | 92.4 | 1076.0 | 10.2 | 5.6 | 178.1 |
| XII | 1 | 96.0 | 105.7 | 1260.5 | 9.3 | 6.8 | 183.0 |
| XIII | 5 | 151.7 | 80.7 | 692.5 | 15.6 | 3.1 | 168.2 |
| XIV | 4 | 681.5 | 300.6 | 809.8 | 16.1 | 4.1 | 133.4 |
| XV | 5 | 1158.4 | 670.7 | 965.6 | 15.4 | 4.7 | 137.0 |
| XVI | 14 | 94.8 | 64.1 | 824.3 | 12.3 | 3.3 | 210.1 |
| XVII | 10 | 150.7 | 134.2 | 869.9 | 14.8 | 3.3 | 216.3 |
| XVIII | 17 | 687.7 | 436.2 | 961.2 | 13.3 | 3.5 | 201.5 |
| XIX | 20 | 521.6 | 355.2 | 1168.4 | 12.1 | 2.4 | 256.1 |
| XX | 6 | 1304.6 | 228.9 | 661.4 | 16.8 | 2.5 | 106.6 |
| XXI | 11 | 844.8 | 291.1 | 769.9 | 16.3 | 1.5 | 185.8 |
| XXII | 30 | 309.3 | 184.9 | 699.8 | 14.1 | 0.6 | 334.0 |
| XXIII | 5 | 585.7 | 506.7 | 779.7 | 14.5 | 0.3 | 339.9 |

Lavanduletea groups, as is also the case in the Lusitanian area, due to their Mediterranean climates.

Ordination diagrams

Results of the DCA showing relationships between the climatic and floristic data are presented in Fig. 3. The diagrams correspond to a biplot of the first and second axes. First, a DCA with all the taxa involved in heathland communities was carried out (Fig. 3a). Axis 1 is related to the inverse of summer drought (Ios) and thermicity (It): both parameters are negatively correlated. The number of associations (asoc) is also positively correlated with thermicity. Axis 2 is positively linked to continentality (Ic) and negatively linked to annual precipitation (Pa), although the latter has less influence in the ordination. The 23 sectors were grouped on the basis of their floristic similarity, geographical distribution and correlation with climatic variables. Specifically, five groups were formed: Scandinavia, Inland sectors, the British Isles and Brittany, France and Iberia and Morocco (Fig. 1).

The Iberia and Morocco group is located on the right side of axis 1, reflecting their thermicity and syntaxonomic richness. Sectors XXII and XXIII under a Mediterranean climate are strongly correlated with this parameter. The other sectors are on the left side of axis 1, which indicates their relation to lack of summer droughts. Scandinavian sectors I and III are highly correlated with Ios. The Inland sectors group includes the most continental ones (V, XIV and XV) correlating with Ic. In contrast, the most oceanic sectors, including those of the British Isles and Brittany, are correlated with annual precipitation.

The other two diagrams of Fig. 3 (B and C) correspond to DCA with *Calluno-Ulicetea* taxa (Fig. 3b) and with species of the other ecological groups (excluding those of *Calluno-Ulicetea*) (Fig. 3c). The variations observed between these three diagrams in terms of distribution of the points are moderate considering the differences in the set of species used to run the program at each time. This indicates that the information contained in the floristic composition of genuine heathland species (*Calluno-Ulicetea*) is not essentially the same as that contained in the set constituted by the rest of the species; the accompanying species are more biogeographically discriminant than the genuine heathland species. This could be due to floristic unity in the origin and ecological requirements of this group of plants. Only Ibero-Moroccan sectors are clearly defined by genuine heathland species, due to the

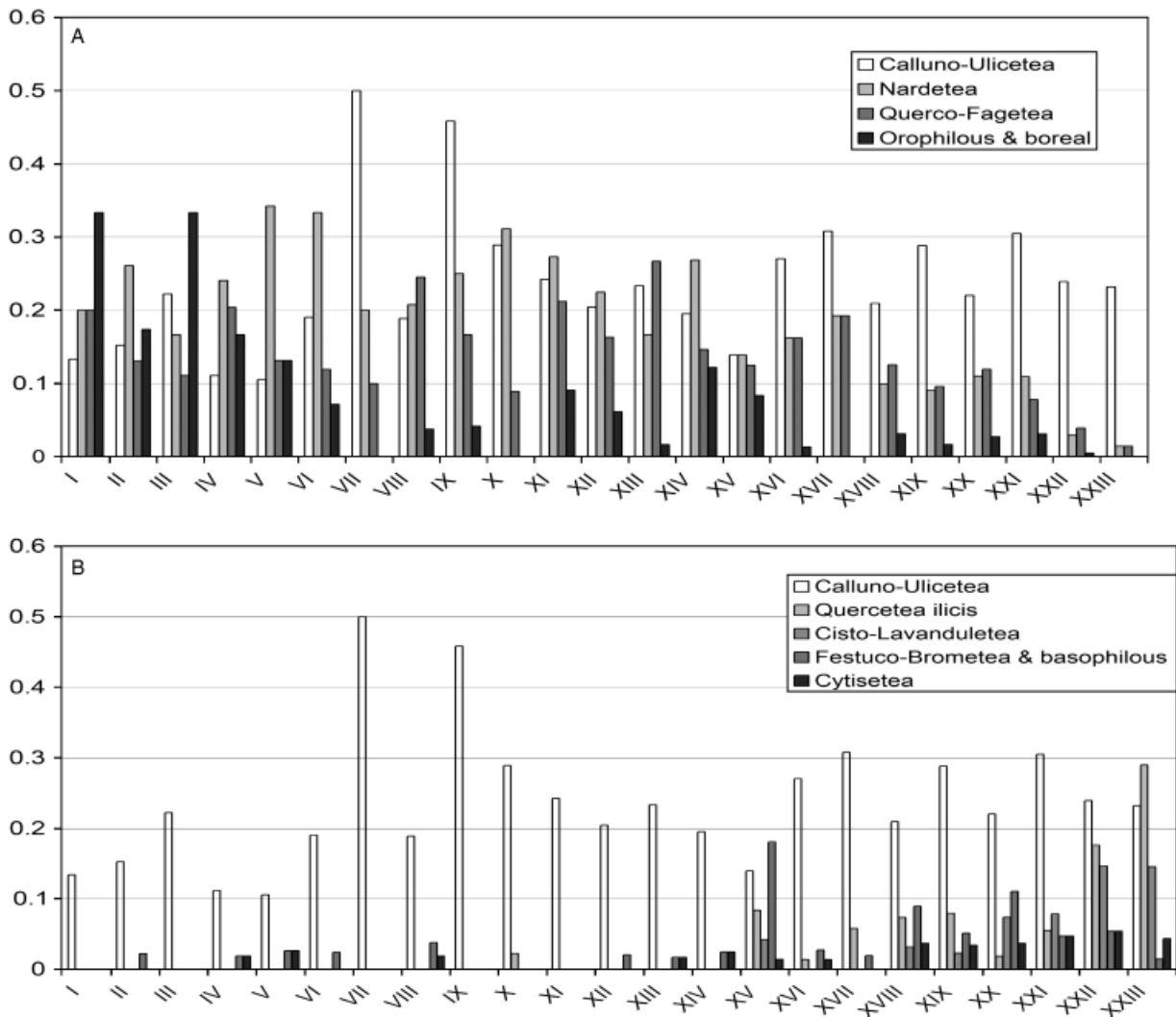


Fig. 2. Proportion of the species belonging to different ecological groups in relation to the total number of taxa present in each sector. (a) Proportion of *Nardetea*, *Quercu-Fagetea* and Orophilous and boreal species in comparison with *Calluno-Ulicetea* species. (b) Proportion of *Quercetea ilicis*, *Cisto-Lavanduletea*, *Cytisetea* and *Festuco-Brometea* & basiphilous species in comparison with *Calluno-Ulicetea* species.

significant number of endemic taxa occurring in these areas. With regard to the diagrams, it should be noted that the difference in ordination of the sectors is related to continentality, whereas their position in relation to It and Ios hardly differs. The classified groups are better defined in the diagram shown in Fig. 3c.

Discussion

In general, heathlands occur under oceanic conditions, with high rainfall and low annual temperature oscillation. They avoid extremely low

winter temperatures and thus are absent from boreal regions and high mountains, as well as from continental areas. In southern areas, they can live at mid-mountain elevations but never at subalpine levels. These climatic features are very similar to those reported by Gimingham (1972), although in his work heathlands from areas with summer drought (W Iberian Peninsula and N Africa) or slightly more continental areas (Subatlantic Europe and Pyrenees) were excluded. The affinity with climatic oceanic conditions could link the distribution of this vegetation type to this trend, and fluctuations in continentality may have largely determined the variations in geographic distribution of heathlands in

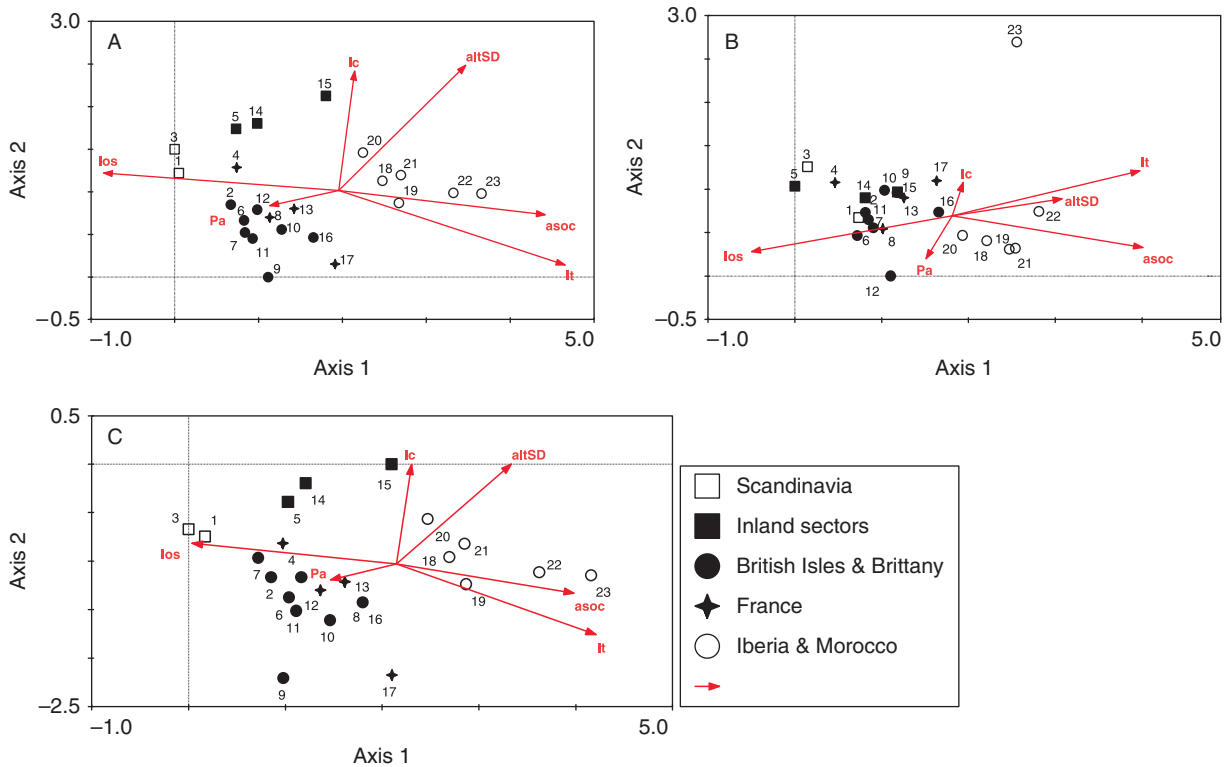


Fig. 3. Detrended correspondence analysis (DCA) of the 23 sectors, climatic data, association number and altitude standard deviation. (a) With all species of the matrix; (b) with only *Calluno-Ulicetea* taxa; (c) with all ecological group taxa except *Calluno-Ulicetea*.

the past. If in the future continentality decreases (Río et al. 2005a, b; Río & Penas 2006a, b), heathlands could even be favoured, but a predicted decrease in rainfall for southern Europe (Castro de et al. 2005) would severely restrict their range.

It is clear that in the southern part of their range, heathlands can withstand a quite severe summer drought, if annual rainfall is high enough to compensate for it, or in edaphically compensated biotopes. The current floristic optimum of this vegetation lies more in the south than the north, a fact partially explained by it having been relatively little affected by past glaciations (Grubb 1987), and suggesting that its northern expansion is recent and was undertaken by those species having the broadest ecological range, such as *Calluna vulgaris* and *Erica cinerea*. These heather species are known to have a long-term-persistent seed bank (Piessens & Hermy 2006) and thus are able to survive unfavourable environmental conditions. It has been reported that *Calluna vulgaris* might have survived in two regions during the last glaciation events: SW Europe and S Britain (Mahy et al. 1999). The current disjunctive distribution in NW Iberia and W Ireland of other heather species, such as *Erica mackaiana* and

Daboecia cantabrica, suggests the same role for these areas, as refuges during Pleistocene ice ages (Mitchell & Watts 1970). This has prompted studies of the morphological homogeneity of species such as *Daboecia cantabrica* that seems to be quite homogeneous across its geographical range (Fagúndez & Izco 2004). Such a distribution pattern and the concentration of genuine heathland taxa in the south suggest a southern optimum and a southern refuge area for this flora and vegetation during Pleistocenic ice ages.

Western Iberia (XIX, XXII; Table 1) is the richest area in terms of total number of species (Table 1); this richness is partly due to the diversity of habitats where heathlands can develop, which allows a large number of heath associations to be distinguished in this area (Rivas-Martínez et al. 2001). The high proportion of *Calluno-Ulicetea* taxa in relation to taxa of other ecological groups may indicate that the most genuine heaths are those of the Iberian sectors, and thus heathlands, in a phytocenotic sense, have their optimum in these areas. However, it must be remembered that this analysis is only based on absence–presence data, and in many heathlands from northern areas, while they

only represent a low proportion, the cover of *Calluno-Ulicetea* species is extensive. In these areas many orophilous and boreal taxa, as well as species from *Nardus stricta* L. grasslands, participate in heaths (Table 1).

The location of the sectors in Fig. 3(a–c) indicates that the most important climatic variables influencing the floristic composition of heaths are thermicity (It) and summer drought (Ios), which are also the main climatic variables related to floristic richness (Table 1). Thermicity has already been reported to be the main climatic factor in the Iberian Peninsula heathlands (Loidi et al. 2007). The results in Fig. 3 indicate that the distribution pattern of the biogeographic sectors in relation to climatic variables is quite similar when using different species sets; therefore, the biogeographic patterns extracted from the genuine heath plants are comparable to those extracted from the accompanying flora, as reported by Loidi et al. (2007).

In the southern part of the study area, i.e. Lusitania and N Morocco, heathlands occur in small territories and are much less common than in other areas having a temperate climate with summer rain, but they contain a high proportion of endemic taxa in their genuine flora (Arroyo & Marañón 1990). This indicates that the Mediterranean climate-adapted heathlands (Benzler et al. 1998) have high diversity and rich endemic taxa due to the climatic stress of the summer drought, as compared with heathlands of other N European territories (Rivas-Martínez 1979; Galán de Mera & Vicente Orellana 1996), and suggests that heathlands were once much more extensive than they are now in these regions; currently they can be considered as relict vegetation (Pérez Latorre et al. 2007).

A large part of this heathland vegetation has an anthropogenic origin and is linked to Neolithic or earlier human expansion in W Europe. The spread of European heathlands through wildfires has been widely documented (Bullock & Webb 1995; Mallik 1995; Calvo et al. 1998, 2002b, 2005; Yallop et al. 2006), although this was combined with grazing and mowing as part of a traditional system of land use that corresponds to a particular disturbance regime (Arroyo & Marañón 1990; Luis et al. 2000; Calvo et al. 2002a, c; Paula & Ojeda 2006). Hence, the conservation strategies for these heathlands, in terms of maintaining their extent and diversity levels, probably needs to involve prescriptive burning, as fire has the clear effect of maintaining heaths in a constant state in terms of species diversity and community structure over time (Britton & Fisher 2007).

Conclusions

Genuine Atlantic heath flora has its optimum in the NW Iberian Peninsula. Northwards, it reaches Scandinavia and Scotland but gradually becomes impoverished and mixed with boreal heath flora and *Nardus stricta* grasslands (*Nardetea*). Southwards, heathlands reach N Morocco but suffer severe restrictions due to Mediterranean drought conditions and remain restricted to mountains or exceptionally rainy areas in which distribution is patchy. The impoverishment in Atlantic-European species parallels the presence of endemics. The accompanying species belong to Mediterranean units such as *Quercetea ilicis* or *Cisto-Lavanduletea*.

The ordinations show that the main climatic factors determining heathland floristic distribution are thermicity (It) and summer drought (Mediterranean character, Ios). Similar patterns are observed in ordinations when using all the species, only the genuine heathland species (*Calluno-Ulicetea*), or all the species except genuine heathland species. Biogeographical information contained in the different species groups of a particular vegetation type is highly redundant but is extremely indicative of actual environmental (climatic) conditions and of historic events and evolution.

The optimal conditions for heath vegetation are found in NW Iberia, where summer drought is moderate and thermicity is high. This suggests that its northern expansion is recent and has been undertaken by species having the broadest ecological range, such as *Calluna vulgaris*. The southern territories seem to have had a role as refuges during Pleistocene ice ages.

Acknowledgements. This study was carried out with financial support from the Basque Government, General Funds for Research Groups, IT299-10, and the Spanish Government CGL2009-13317-C03-02. We appreciate the suggestions and amendments of Milan Chytrý and two anonymous reviewers.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Bibliographic sources surveyed to build the floristic data in Table 1 and the number of relevés from each of the sectors.

Photo S1. *Daboecia cantabrica*.

Photo S2. *Erica cinerea* I.

Photo S3. *Erica cinerea* II.

Photo S4. *Erica tetralix* I.

Photo S5. *Erica tetralix* II.

Photo S6. Heathland in the Basque Country.

Photo S7. Heavily grazed heathland in the Basque Country.

Photo S8. Montane heathlands in the Basque Country.

Photo S9. Mown heathland in the Basque Country.

Photo S10. Mt. Gorbea July 1999, Burned heathland in the frame of traditional management in the Basque Country.

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Received 27 February 2009;

Accepted 20 June 2010.

Co-ordinating Editor: Dr. Milan Chytrý.