



Phytogeographical relationships among high mountain areas in the Baetic Ranges (South Spain)

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ABSTRACT

The Mediterranean area is regarded nowadays as one of the hot-spots of world biodiversity. The Baetic ranges in Spain have such a large number of endemic plant taxa that the territory has been recognized as a well-defined biogeographical unit. These endemic taxa tend to concentrate on disjunct highland areas that have been described consequently as 'highland islands'. Despite the importance and complexity of these sites, the research carried out so far has produced only descriptive classifications. These approaches overlook the relationships between the sites and do not serve to identify the main centres of endemism. Herein, multivariate analysis techniques (cluster analysis and reciprocal averaging) and the parsimony analysis of endemism (PAE), applied to the 222 orophilous endemic taxa of the Baetic ranges, have been used to reveal the floristic similarities between the areas involved,

to identify the centres of endemism and to re-assess the previous classifications. Four centres of endemism are defined, one siliceous and three calcareous. The most outstanding feature in the Baetic ranges is precisely the floristic difference between siliceous and calcareous mountains. Calcareous territories extend along a SW–NE axis in line with the oceanic–continental gradient. The nature of the soil in the vast siliceous and calcareous–dolomitic territories of the Sierra Nevada is probably the cause of the remarkable floristic diversity. Not surprisingly, in our analysis these areas stand out as centres of endemism. We conclude that previous biogeographical classifications of the ranges are too rigid and do not properly reflect the floristic similarities of the area under study.

Key words biogeography, centres of endemism, flora, multivariate analysis, PAE, preservation areas, Spain.

INTRODUCTION

Since De Candolle used, for the first time in 1820, the term 'endemic' in a botanical sense to refer to species of restricted distribution, many attempts at classifying these taxa have been made (Favarger & Contandriopoulos, 1961). Despite these attempts and the worldwide use of the term, an exact definition is still a matter of contention (Anderson, 1994). Nevertheless, the distribution and conservation of endemic plant taxa are frequent topics of scientific research.

Given that there exist well-defined areas where endemic taxa tend to occur, i.e. endemics are not randomly distributed, a number of ideas have been suggested to account for their distribution. A global approach supports the idea that the number of endemic species tends to increase with decreasing latitude (Gentry, 1986), although the areas of Mediterranean climate conditions do not comply well with this idea (Cody, 1986; Platnick, 1992). Data on the number of species and

occurrence of endemics have been used in the regions of Mediterranean climate to map the sites worthy of preservation (Mooney, 1990; Médail & Quézel, 1997, 1999). Many authors have noted the importance of the Baetic ranges because of the diversity of their flora and the number of endemic species (Sainz de Ollero & Hernández Bermejo, 1985; Gómez Campo, 1987; Rivas Martínez *et al.*, 1991; Moreno Saiz & Sainz de Ollero, 1992; Molero Mesa, 1994; Domínguez *et al.*, 1996).

A different pattern has been observed with regard to isolated areas and biotopes, however complex and varied the origin of the endemics may be. This second hypothesis states that endemic species tend to be concentrated on islands, mountain peaks and unusual edaphic outcrops, such as imbalanced substrates (Kruckeberg, 1969, 1992; Given, 1981; Gentry, 1986). Gómez Campo (1985, 1987) and Médail & Verlaque (1997) have also suggested that high environmental stress, such as rocky terrains and scree, tend to produce a higher number of endemic species.

Conditions also become more demanding when these bizarre requirements take place on high mountains (Papanicolaou

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et al., 1983). In fact, many researchers have observed that endemic plant species tend to occur in high mountains (Hedberg, 1969; Valentine, 1972; Kruckeberg & Rabinowitz, 1985; Gentry, 1986). There is, for example, a direct correlation between altitude and the occurrence of endemic plants in the Canary Islands (Cains, 1944), which supports the idea that topographical variability plays an important role in promoting endemic species.

The high mountain endemic species of the Baetic ranges are used here as a criterion to analyse the relationships between disjunct high mountain areas. Taking into account that 60% of the Iberian endemic plants occur in high mountain habitats (Domínguez *et al.*, 1996), the number and importance of the taxa under study are considerable. We have aimed not only at describing and interpreting the spatial patterns of distribution of the high mountain endemic species in the Baetic ranges, but also at comparing these results with the data of other surveys that have dealt with the endemic flora. Previous biogeographical surveys, by Sainz de Ollero & Hernández Bermejo (1985) and by Rivas Martínez *et al.* (1991, 1997) offer only simple classifications in which areas considerably different in diversity are ascribed to the same hierarchical category. The ecological system by Rivas Martínez *et al.* (1997) also fails to meet the fundamental requirement of natural biological classification, i.e. the designation of explicit empirical statements of relationships that allow for falsification. Despite

the amount of research published on the matter, the current biogeographical typology of the Baetic ranges so far is too rigid and imprecise and does not mirror the true relationships between the different areas. This deficiency in our current biogeographical terminology for properly expressing the connections between centres of endemism compares well with the insufficiency of classic taxonomy for accurately describing phylogeny (Humphries & Parenti, 1999). For example, none of the previous surveys mention the clear floristic dissimilitude between siliceous and calcareous areas. This, together with other biogeographical features, will come to light only by means of a holistic approach aiming at the identification of the centres of endemism and, subsequently, formulating a long overdue preservation policy.

AREA UNDER STUDY

The Baetic ranges are located in the south of the Iberian Peninsula and comprise large areas of Andalusia, Murcia, Albacete and Alicante. Mountain peaks over 2000 m can be found over the whole of this extensive territory, except in Alicante. The present paper involves the study of 21 areas (Table 1), among which the localities > 1800 m asl are mostly disjunct, although some are close to each other. Despite their proximity, the siliceous and calcareous sites of Sierra Nevada and Filabres were considered separately in our analyses.

Table 1 Localities under study. The table shows the edaphic profile, abbreviations used in the text and in the figures, biogeographical sectors (Rivas Martínez *et al.*, 1997), number of Baetic endemic taxa (BE), exclusive endemic taxa (EE), oromediterranean belt area in ha (OS) and highest altitude in m (H)

Geology	Abbreviation	Sites	Sector	BE	EE	OS	H
Calcareous	GRA	Grazalema	Rondeño	14	0	0	1665
	NIE	Nieves		15	1	240	1918
	LOJ	Loja		8	0	0	1671
	LÚJ	Lújar	Alpujarreño–Gadorense	16	0	57	1824
	GAD	Gádor		37	7	3 927	2240
	TEJ	Tejeda	Malacitano–Almijarensis	52	2	126	2065
	ALM	Almijara		38	0	114	1832
	SNC	Calcareous Sierra Nevada		71	5	1 138	2450
	HAR	Harana	Subbético	31	0	948	1943
	MGN	Mágina		62	5	3 390	2167
	HOR	Horconera		21	1	0	1570
	CZO	Cazorla		72	3	26 096	2028
	CST	Castril		54	0	10 285	2133
	SAG	La Sagra		64	0	1 062	2383
	CBR	Cabras		32	0	1 986	2081
	REV	Revolcadores		35	1	639	2001
	MRI	María	Guadiciano–Bacense	46	3	1 473	2045
	FIC	Calcareous Filabres		25	0	403	2080
	BAZ	Baza		52	0	5 263	2236
	Siliceous	FIS	Siliceous Filabres	Nevadense	26	1	10 481
SNS		Siliceous Sierra Nevada		94	54	54 811	3482

From a biogeographical point of view, all the sierras considered here have been included in the units of the Holarctic kingdom, the Mediterranean region and the Baetic province (Rivas Martínez *et al.*, 1997). Within the limits of this last chorological unit, five (Sainz de Ollero & Hernández Bermejo, 1985) or seven (Rivas Martínez *et al.*, 1997) subunits or sectors have been distinguished. These chorological units will be used frequently in this paper (see Table 1).

Most of the localities concerned are under the protection of the Andalusian law, which has declared Cazorla, Tejada, Almjara, Nieves, Baza, Mágina, Castril, María and Sierra Nevada as *Parques Naturales* (Natural Parks). The highest peaks of the latter have also been conceded the protection of a *Parque Nacional* (National Park). Some other areas worthy of preservation have unfortunately been overlooked (La Sagra, Gádor), despite the considerable value of the flora involved and the appeals of researchers (Mota *et al.*, 1996; Giménez, 2000).

MATERIALS AND METHODS

Species distribution data

Mapping oromediterranean areas

In order to carry out our survey we chose 21 high mountain areas which, for the most part, lie approximately along the boundary of the oromediterranean belt, i.e. over 1800 m high. This territory is shown on the map by Rivas Martínez (1987) on a 1 : 400 000 scale. Two reasons led us to include in our survey three sites that do not have peaks over 1800 m and, consequently, do not have a true oromediterranean belt (Grazalema, Horconera and Loja). First, due certainly to microclimatic effects, some of the endemic taxa under study occur on these peaks (Mota, 1990). Secondly, the inclusion of these sites makes our biogeographical analysis more comprehensive and valuable, because by so doing all the chorological units or sectors recognized previously encompass two or more sites. As can be seen in Table 1, in the following analysis one of the seven sectors considered by Rivas Martínez *et al.* (1997) is missing because the Hispalense sector, which coincides with the valley of Guadalquivir river, has no highlands.

Flora catalogue

The data of the 19 calcareous sites included in our analysis (Table 1) have been taken from Mota (1990): Nieves and Cabras; López Guadalupe (1974): Lujar; Giménez (2000): Gádor; Laza Palacios (1946) and Nieto (1987): Tejada and Almjara; Pérez Raya (1987): calcareous Sierra Nevada; Socorro (1977): Harana; Cuatrecasas (1929): Mágina; Gómez Mercado (1989): Cazorla; Gómez Mercado *et al.* (2000): Horconera; Arrojo (1994): Castril; Negrillo (1980):

La Sagra; Sánchez-Gómez *et al.* (1998) and Mota (1990): Revocadores; Cueto & Blanca (1997): María; Peñas (1997): calcareous Filabres; Blanca & Morales (1991): Baza; Martín Osorio (1993): Grazalema; Marin Calderón (1978): Loja. As sources of general information the following were used: Castroviejo *et al.* (1986–93), Rivas Martínez *et al.* (1991), Valle *et al.* (1989a,b), Navarro *et al.* (1990), Gómez Mercado *et al.* (1997). This body of data, with 157 endemic taxa, has been completed with the data of the siliceous sites of Sierra Nevada (Molero Mesa & Pérez Raya, 1987) and Filabres (Peñas, 1997). The total number of endemic taxa is 222. The presence (1) or absence (0) of endemic taxa was arranged in a matrix which has been used for all subsequent analyses and is available from the authors. All the taxa recorded in this matrix comply with the following criteria: their distribution is restricted almost entirely to the Baetic ranges and their occurrence has been recorded in the oromediterranean belt or over 1800 m.

Phytogeographical analysis

Numerical analysis of plant distribution has been recognized for some time as a potentially powerful adjunct to traditional methods of biogeography (Birks, 1987). Cluster analyses were used to classify the highland localities. Several agglomerative hierarchical procedures (furthest neighbour, weighted average and Ward's method) were performed to define groupings (McGarigal *et al.*, 2000; Podani, 2000). Such methodological features are considered here to be particularly useful in dealing with biogeographical classification. The similarity between the highland localities was calculated using Sorensen's similarity index and relative Euclidean distance (Hubálek, 1982; Kenkel & Booth, 1987; Podani, 1994).

Reciprocal averaging (RA) was performed in order to examine biogeographical relationships among localities. Comparison of the results yielded by the previous method was made in order to minimize the risk of possible misinterpretations derived from the inherent assumptions of each analytical method (Jongman *et al.*, 1995; Legendre & Legendre, 1998; Waite, 2000). To carry out a preliminary analysis we have used the following programmes: SYN-TAX 5.0 (Podani, 1994) and PC-ORD 3.0 (McCune & Mefford, 1997).

A parsimony analysis of endemism (PAE) (Rosen, 1988) was applied to the presence/absence of the 222 taxa of vascular plants from the 21 localities. The PAE groups areas (analogous to taxa) by their shared taxa (analogous to characters) according to the most parsimonious cladogram (Crafft, 1991; Myers, 1991; Morrone, 1994, 1998; Posadas, 1996). PAE cladograms were generated using PAUP 4.0 (Swofford, 1998), with a hypothetical outgroup area containing no taxa as the root. The most parsimonious trees were found using a heuristic search with 10 replicates of random stepwise addition. The eight shortest trees were found and then the strict consensus rule was computed.

RESULTS AND DISCUSSION

Table 1 shows some basic data of the 21 selected areas, such as number of Baetic endemic taxa, number of exclusive endemic taxa for each site, oromediterranean area and highest altitude. The area with the largest number of endemic taxa is the siliceous core of Sierra Nevada, with 94 species, 54 of which are exclusive. Two calcareous sites, Sierra Nevada and Cazorla, have an outstanding number of endemic plants (around 70) and La Sagra and Mágina have comparable records. As can be seen, in many of these sites the oromediterranean area is extremely limited (Lújar, Almjara, Nieves) or nonexistent (Loja, Horconera, Grazalema), in contrast to the region of Cazorla or the siliceous Sierra Nevada.

The dendrograms obtained (Fig. 1) show the floristic biogeographical similarities between the sites. Most of the groups (Loja–Lújar, Tejada–Almijara–calcareous Sierra Nevada, Harana–Mágina, María–Baza and calcareous Filabres–Gádor) are shared by all of them. In addition, there are three

more, even more remarkable, groups. Each of these three groups intersects, in some of the dendrograms, with the rest at the last fusion. This arrangement can mean only a great dissimilitude in the polythetic agglomerative hierarchical clustering. The set Grazalema–Nieves, which is intersected by Horconera–Loja–Lújar, is separated from the rest of ranges in the dendrogram shown in Fig. 1(a) and is easily recognizable as such in all the other analyses. The second dendrogram (Fig. 1b) shows Cazorla and its neighbouring territories (i.e. Castril–La Sagra–Cabras–Revolcadores) as an independent site. Although in the other two dendrograms the similarity of these ranges with the rest of the localities under study varies, their coherence as a discrete subset is beyond doubt. Finally, as Fig. 1c shows, the siliceous areas of the Sierra Nevada and Filabres are clearly separated from the other localities. This same conclusion arises from all the other analyses: the difference between the siliceous and the calcareous territories is one of the most outstanding biogeographical features of the Baetic ranges.

Previous surveys (Rivas Martínez *et al.*, 1997) tended to associate Mágina and Harana with the set of Cazorla (Cazorla–Castril–La Sagra–Cabras–Revolcadores). However, as Fig. 1b,c shows, these two sites are usually linked to the set that we call Malacitano–Almijarese (Tejada–Almijara–calcareous Sierra Nevada). Other groups, such as that of María and Baza or that of Gádor and the calcareous Filabres, appear in different ways: sometimes they are associated with the set of Cazorla (Fig. 1a,c), sometimes with the set of the calcareous Sierra Nevada (Tejada–Almijara–Sierra Nevada) and sometimes they appear mutually associated (Fig. 1b).

Cluster analyses unequivocally define four groups: Rondeño (Grazalema–Nieves), Malacitano–Almijarese (Tejada–Almijara–calcareous Sierra Nevada), Bético–Cazorlense (Cazorla–Castril–La Sagra–Cabras–Revolcadores) and siliceous Nevadense (Sierra Nevada–Filabres). With the exception of the group of Mágina–Harana, which is closely related to the calcareous Sierra Nevada, the rest of the localities included in our survey have dubious floristic similarities with each other.

The RA (Fig. 2) clearly separates along the first axis the siliceous ranges from the calcareous ones, an outcome in line with the results of Ward's minimum-variance linkage (Fig. 1c). The second axis has two clearly distinct extremes: Rondeño, i.e. Nieves–Grazalema, on one hand, and Bético–Cazorlense, i.e. Cazorla–Castril–La Sagra–Cabras–Revolcadores, on the other hand. The rest of the localities can be seen in varied intermediate locations, with the Malacitano–Almijarese group (Tejada–Almijara–calcareous Sierra Nevada) at the central point of this axis. While Loja–Lújar appear between Rondeño and Malacitano–Almijarese, for example, all the others tend to appear near the extreme of Cazorla.

Like the cluster analyses, the RA defines four groups. Three of them, Nevadense (siliceous Sierra Nevada and Filabres),

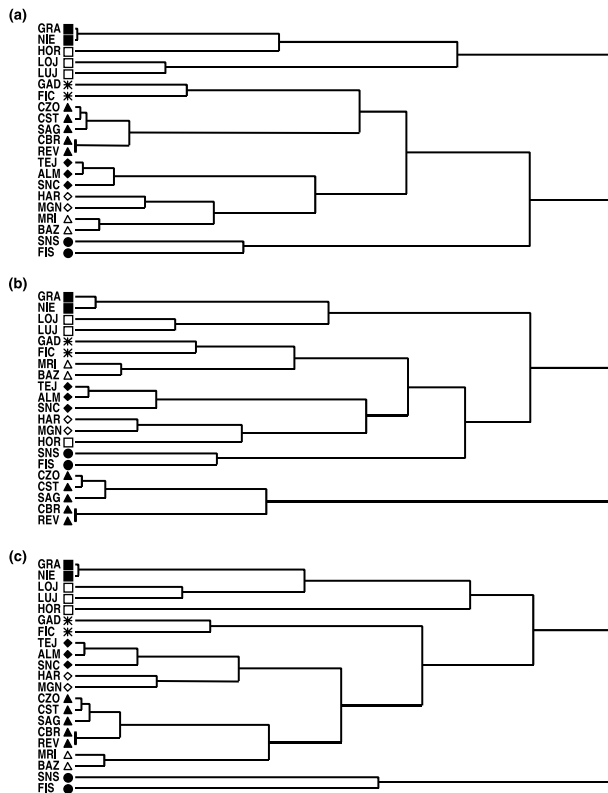


Fig. 1 Dendrograms of the sites based on the presence/absence of the 222 endemic taxa. Symbols refer to the eight groups common to all the dendrograms (i.e. GAD–FIC, MRI–BAZ, HAR–MGN, ...). Clustering strategy and similarity (distance) measure: (a) furthest-neighbour and Sorensen index, (b) unweighted group average and Sorensen index, and (c) Ward's method and relative Euclidean.

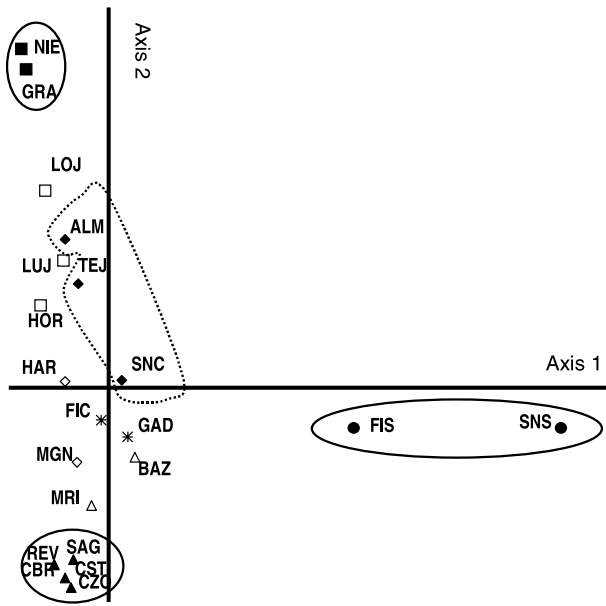


Fig. 2 Plot of the first and second axis from reciprocal averaging analysis of the presence/absence data for the taxa in each locality. The symbols are those used in the dendrograms. The continuous lines represent groupings identified in this analysis (clearly separated from the rest and located at the extremes of the axes) and in the previous dendrograms. The dashed lines encircle the Malacitano–Almijarensis group (SNC–TEJ–ALM), easily recognizable in the dendrograms and the PAE. Its central position in the diagram mirrors its geographical situation in the heart of the Baetic ranges.

Rondeño (Nieves–Grazalema) and Bético–Cazorlense (Cazorla–Castril–La Sagra–Cabras–Revolcadores) are obvious. The fourth is not so well defined, although the group Malacitano–Almijarensis (calcareous Sierra Nevada–Tejeda–Almijara) can be considered as the central core of a complex in which the rest of the sites are arranged either towards the group Rondeño or the group Bético–Cazorlense.

PAE retained eight most parsimonious trees, with 464 steps, a consistency index score of 0.4784 and a retention index score of 0.5624. In the strict consensus tree two regions form a basal dichotomy: siliceous and calcareous ranges (Fig. 3). The relative distinctiveness of the siliceous baetic high mountain flora in a well-supported clade is also confirmed by the preceding analyses. Significantly, however, this clade includes two calcareous sites (Filabres and Gádor). This is due undoubtedly to the large number of taxa that these sites share. The calcareous sites of lower altitudes, with nearby siliceous territories that possess a large oromediterranean area, are probably influenced by the flora of the latter which tends to invade neighbouring areas, the more so when they are decarbonated habitats such as dolomites (Mota *et al.*, 1993) or sinkholes (Mota, 1990).

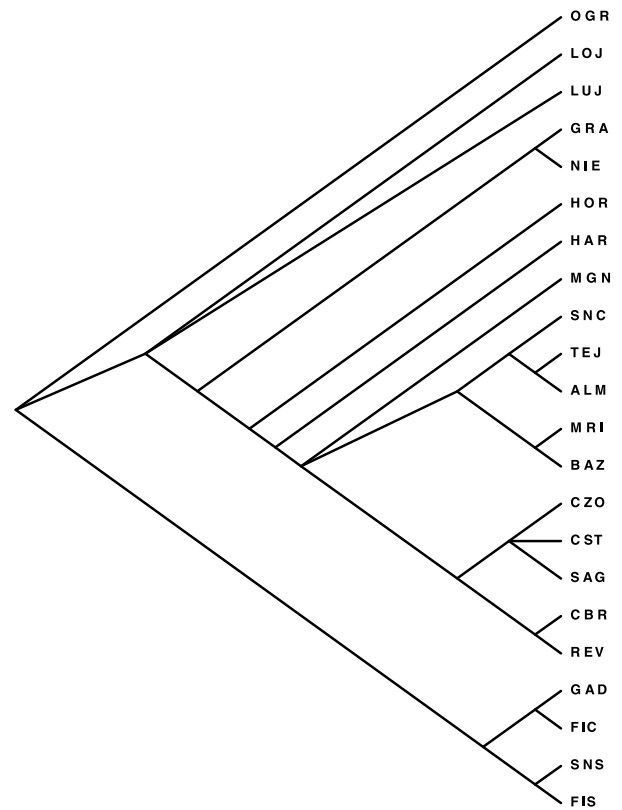


Fig. 3 Strict consensus tree of eight equally parsimonious trees for the 20 localities based on the presence/absence of the 222 orophilous endemic taxa of each sierra.

The rest of the calcareous sites form the second large group of the cladogram (Fig. 3). Within this group, three distinctive clades were defined: Rondeño (Nieves–Grazalema), Malacitano–Almijarensis (calcareous Sierra Nevada–Tejeda–Almijara) and Bético–Cazorlense (Cazorla–Castril–La Sagra–Cabras–Revolcadores). The first of these, encompassing the ranges of Grazalema and Las Nieves, is the most distinctively basal group. Despite the scarce oromediterranean area of these two ranges, their endemic flora is remarkable (Domínguez, 1988; Pérez la Torre *et al.*, 1998). The ranges of Loja and Lújar are not so clearly defined in the clade of the calcareous ranges. The ranges of María and Baza appear in a clade associated with the Malacitano–Almijarensis (calcareous Sierra Nevada–Tejeda–Almijara). When compared to this complex and to the Bético–Cazorlense (Cazorla–Castril–La Sagra–Cabras–Revolcadores), the ranges of Mágina and Harana have a peripheral position in the cladogram. The PAE of localities considered separately resulted in topologies with clades that only in part matched Rivas Martínez's phytogeographical units (Rivas Martínez *et al.*, 1997). The hierarchical arrangement of geographical areas is a useful way of depicting

floristic data. However, the current analysis suggests that Rivas Martínez's classification is too crude. The hierarchy of the floristic areas (choria) of the Baetic ranges should first differentiate a siliceous unit (encompassing the metamorphic centres of Sierra Nevada and los Filabres) as distinct from the rest of the mountains, in which calcareous rocks, such as limestones, dolomites and marbles prevail. In line with the suggestion by Sainz de Ollero & Hernández Bermejo (1985), in this latter unit the north-eastern territories of Cazorla–Castril–La Sagra–Cabras and Revolcadores are clearly distinct from all the others.

There is, however, no undisputable formula for classifying floristic areas. Perhaps, it would be more realistic to assume a complex net that allows simultaneously more than one biogeographical relationship between any pair of given chorias (Craw *et al.*, 1999). From this point of view, we conclude that the orophilous flora of the Baetic ranges have four centres of endemism: (1) Rondeño (Nieves–Grazalema), (2) Malacitano–Almijarensis (calcareous Sierra Nevada–Tejeda–Almijara), (3) Bético–Cazorlense (Cazorla–Castril–La Sagra–Cabras–Revolcadores) and (4) Nevadense–silíceo (Sierra Nevada–Filabres); the first three are calcareous and the last siliceous. They include 106 endemic taxa absent in the rest of the sites, i.e. 47.8% of the endemic taxa of the Baetic ranges. Of these 106 taxa, 66 (i.e. 80% of the local endemic taxa) are exclusive to one site. The rest of the highlands include only 17 taxa exclusive to one site, most of them in Gádor, Mágina and Sierra de María. With this distribution of endemic taxa, some of the former biogeographical units clearly poor in endemic species, such as Alpujarreño–Gadorensis or Guaciano–Bacense (Rivas Martínez *et al.*, 1997) are disputable. As far as the number of endemic species is concerned, they can hardly be compared with the four units surveyed in this paper. Taking into account that the Sierra Nevada encompasses two of the main centres of Baetic endemic species, it is easy to understand its important role for the preservation of the Mediterranean flora. In addition to the species richness, some mitotypes are present only in the most southerly populations from the Sierra Nevada (e.g. Sinclair *et al.*, 1999). It is vital for conservation purposes to understand the importance of the Baetic ranges as centres of endemism and refugial areas.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/GEB/GEB312/GEB312sm.htm>

Matrix showing the presence (1) or absence (0) of 222 endemic taxa from the 21 highlands that have been used for all subsequent analyses (abbreviations used for localities under study are shown in Table 1).

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