

## Floristic variation, chorological types and diversity: do they correspond at broad and local scales?

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**Abstract.** The relationships between biogeographical patterns and local-scale patterns based on microscale features, such as topoclimate, are well known in plant biogeography. Here we present a method of determining this correspondence using constrained ordination and correlations. We examined compositional gradients at two different scales, biogeographical chorotypes, and diversity. Compositional data (124 taxa × 113 plots) were sampled at four regularly spaced sites in south-eastern Spain. Longitude (LONGI) was used as a spatial variable representing an east–west climate gradient, together with a radiation index (RADIN), elevation, and a disturbance indicator. All factors correlated with the compositional gradients, but the local-topoclimate factor (RADIN) and the broad-scale factor (LONGI) were most important. These two, spatially independent factors were both correlated with the two first ordination axes, and therefore should relate to the same general trend in species-turnover. There was a significant Spearman's rank correlation between the species order along these two gradients. This is interpreted as an ecological self-similar pattern, i.e. coenoclines repeating at

different scales. A consistent order of species along local- and broad-scale coenoclines may indicate that similar operational factors act at several scales, here related to moisture and temperature. The distribution of Mediterraneo–Macaronesian, Mediterraneo–Saharo–Arabian and Ibero–Maghribian species confirmed the correspondence between the broad- and local-scale gradients. The former group decreases in number with increasing aridity along both gradients, whereas the two latter groups increase. A discordant pattern was found with south-eastern Iberian endemics, but this may be explained by several of them being edaphic (saxicolous) specialists. There is a significant decrease in species richness with high radiation, but the expected increase along the longitudinal gradient from west (dry) to east (moist) was not statistically significant. This may be due to the correspondence between high richness and disturbance, both occurring in the middle of the broad-scale gradient.

**Key words.** Biodiversity; canonical correspondence analysis; Mediterranean; partial ordination; plant biogeography; self-similarity; scale.

## INTRODUCTION

The energy resources of ecosystems are ultimately dependent upon the amount of light intercepted. The ecological reasons for variation

in vegetation should be sought not only from the radiation pattern as such, but also from its effect on the temperature and moisture balance that determines vegetation patterns on broad and local scales (Woodward, 1987). A close relationship between floristic variation and the aspect and inclination of slopes, which induce the radiation gradient, has often been documented, e.g.

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in the Middle East (Boyko, 1947), South Africa (Granger & Schulze, 1977), the Iberian Peninsula (Dargie, 1984, 1987), Australia (Kirkpatrick *et al.*, 1988) and the Himalayas (Vetaas, 2000).

This global phenomenon of aspect (i.e. topoclimate) and vegetation gradients also relates to broad-scale biogeographical patterns. For instance, some of the northernmost extensions of European deciduous forests can be found on south-exposed slopes along the fjords of western Norway, whereas boreal forests cover the northern slopes (Aarrestad, 2000). The same occurs in south-eastern Spain, where the Mediterranean evergreen forest is restricted to northern slopes (cf. Zavala *et al.*, 2000), and the northernmost extension of African drought-deciduous *matorral* is found on southern hillsides near the coast (Peinado *et al.*, 1992).

The correspondence between macro-pattern (i.e. geographical distribution) and micropattern (i.e. topographical distribution of species) has been recognized for a long time (Tansley & Chipp, 1926). It has both theoretical and practical importance, because it elucidates community organization and the regulation of species diversity. Boyko (1947) called it the 'geo-ecological law of distribution', which relates to similar concepts such as 'equivalence of sites' (Loucks, 1962; Vetaas, 1992) and 'habitat-constancy' (Walter & Walter, 1953; Miehle, 1989), or niche-constancy (see Discussion).

However, the relationship between microscales and macro-scales has normally been studied for individual species or vegetation types. An explicit comparison of micro- and broad-scale compositional gradients has not been performed. This is probably because plant ecologists and biogeographers have focused on similarities between (i) species or species associations and (ii) relevés or communities. The sequential order of species along a gradient, i.e. *coenocline sensu* Whittaker (1967), can also be analysed by means of ordination and correlation. This allows a more accurate comparison of the different scales, and the degree of correspondence can be expressed statistically (Vetaas, 1997). A consistent order of species along local- and broad-scale *coenoclines* may indicate that similar operational factors act on several scales. This is also important for the species richness of an area. If moist microhabitats occur in the dry end of a broad gradient, and

vice versa, a certain number of species may find refuge in a suitable habitat along most of the broad gradient. This type of heterogeneity is related to the concept of 'mass effect' (Shmida & Wilson, 1985), which may enhance as well as sustain the diversity in an area.

Multivariate methods have been applied to analyse the effect of topoclimate (Dargie, 1987; Vetaas, 1992) and larger biogeographical gradients (Westman, 1983; Ojeda *et al.*, 1996; Ferreyra *et al.*, 1998). Dargie (1987) gave an example of the problems related to topoclimate gradients and the interpretation of the ordination space derived from indirect ordination (e.g. detrended correspondence analysis (DCA); Hill & Gauch, 1980). He emphasized so-called 'oblique' trends, and developed a sophisticated technique to regress ordination axes onto variables such as solar radiation. Nowadays, it is possible to do regression and ordination simultaneously by means of canonical ordination (e.g. canonical correspondence analysis (CCA); ter Braak, 1986).

Canonical ordinations facilitate an explicit scaling of the ordination biplot. This is particularly useful when there are variables representing different spatial extents, e.g. one is scaled to reflect a micropattern such as a topoclimate gradient, and another to reflect a larger biogeographical pattern. If the micropattern repeats along the broad-scale biogeographical gradient, the two gradients may appear as independent (orthogonal) in the ordination space, although the floristic variation may still be related (cf. Vetaas, 1997). This may occur if both patterns are correlated to the same operational factors.

This relationship between micro- and macro-pattern may be more obvious in extreme environments, where moisture and temperature are strong determinants of vegetation gradients. This study comes from an arid to semi-arid mountain range of south-eastern Spain, which is in the same region as the area studied by Dargie (1984, 1987).

Our main aims are to (1) describe the variation in plant species composition, and relate this to spatial variables of different extent; (2) evaluate the hypothesis that species optima along a broad-scale climate gradient are reflected in their position on a local-scale (topoclimate) gradient and vice versa, and (3) elucidate whether the variation in chorological types confirms this hypothesis.

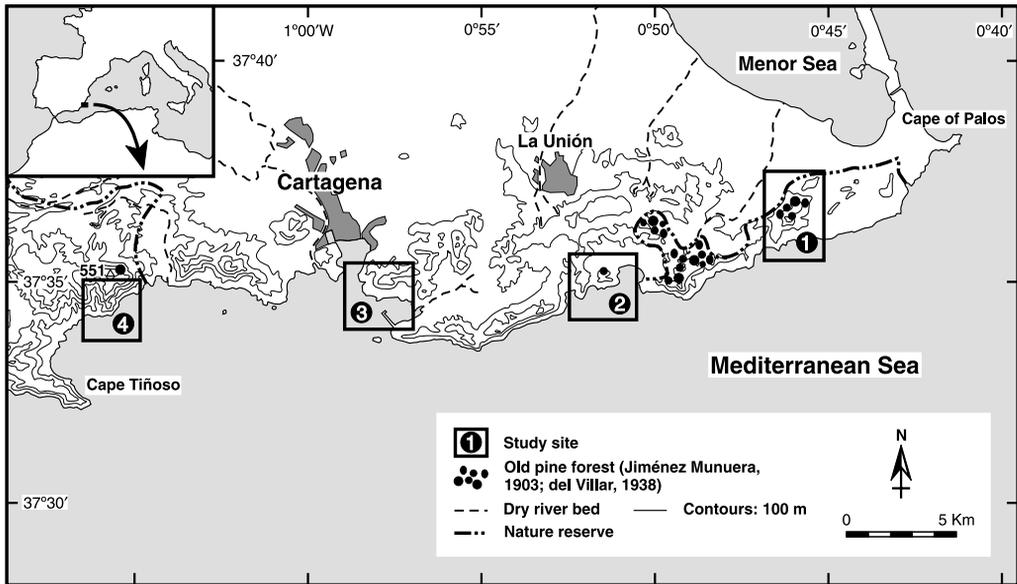


Fig. 1 Location of the study sites (Sierra de Cartagena, south-eastern Spain).

Because the Mediterranean vegetation has a long history of human influence, we also related the same variables to a disturbance indicator.

## MATERIALS AND METHODS

### Study area

The study took place in the Sierra de Cartagena, a mountain range of south-eastern Spain (37°32'–37°38'N and 0°41'–1°11'W) running from east to west close to the Mediterranean Sea (Fig. 1). It is the easternmost mountain range of the Baetic Cordillera *sensu stricto*. Triassic limestones and dolomites are the predominant parent materials, appearing as discontinuous outcrops over a Palaeozoic base of quartzites, slates and mica-schists (Fernández, 1986). Elevation ranges up to 551 m a.s.l., and the relief is precipitous with cliffs and rocky outcrops.

The Cartagena range is located in one of the driest areas in Europe, in a transition zone between Mediterranean and arid subtropical (desert) climates. At its eastern end, mean annual precipitation (MAP) is 350–400 mm (coefficient of variation (CV) is 40–50%), mean

annual temperature (MAT) is around 17 °C and frosts are occasional. In the west, MAP is only 200–250 mm (CV about 35–40%), MAT is greater than 18 °C and frosts are very rare (Ferrer-Castán *et al.*, 2000). The lapse rate is 0.54 °C/100 m, and fogs are frequent. There are cool and humid NE winds (*levante*), whereas the African SW winds (*lebeche*) are warm and dry.

A great part of the Cartagena range has been altered profoundly by opencast mining, particularly in the surroundings of La Unión. However, there are still well-preserved areas of shrubland, open woodlands of *Tetraclinis articulata* (Vahl) Masters, pine forests (*Pinus halepensis* Miller) (Fig. 1), and mixed forest of *P. halepensis-Quercus ilex* L. (cf. Jiménez Munuera, 1903; del Villar, 1938; Esteve Chueca, 1973; Peinado *et al.*, 1992). Our study deals with these preserved areas, which are located partly within nature reserves (Fig. 1).

### Field sampling

Four sampling sites spaced regularly along the Cartagena range (Fig. 1), were selected on limestone and dolomite substrate. At each site (hereafter S1, S2, S3 and S4, from east to west)

one or two hills were chosen (more details are found in Ferrer-Castán, 1994). The sampling design aimed to cover all the eight 45° aspect-intervals (N, NE, E, etc.), but locations where the slope angle was higher than 45° and clearly disturbed sites (e.g. by recent fires) were avoided. Thus the east- and west-facing slopes of S1 and S3 were not sampled. On average five to six plots (10 m × 10 m) were placed at each aspect-interval, but this varied depending on topography and accessibility.

The presence of the seasonally persistent plant species was recorded in each plot, together with aspect, slope angle, elevation and geographical location. Stem counts of *Calicotome intermedia* C. Presl were also recorded (see below). The total number of plots was 113 with a total of 124 species.

### Numerical expression of environmental factors

The longitude of each plot was used as a spatial variable (LONGI), which was assumed to represent the east–west climate gradient along the Cartagena range. Elevation (ELEVA) was used as an indirect variable related mainly to temperature. A radiation index (RADIN) was calculated as a function of aspect, slope inclination and latitude (Oke, 1987). Although some climate data are available from the study area (Ferrer-Castán *et al.*, 2000; New *et al.*, 2002), we chose to use the above indirect variables. This is because the climate estimates would have been based on interpolation from insufficient climate data, where some stations have a short recording period. Another problem is to express the variation at local scale, i.e. topoclimate. This needs detailed measurements with climate data loggers at different aspects and inclinations.

Stem counts of *Calicotome intermedia* in each plot were used as a disturbance index (CALICO) as this shrub species becomes dominant on moderately disturbed sites (Peinado *et al.*, 1992). It seems to be favoured by fire, as is the case with other legumes of the same genus (cf. Tomaselli, 1982).

### Numerical analyses

*Compositional variation and environmental variables* DCA (Hill & Gauch, 1980) was used to estimate the length of species-axes in SD-units (Jongman

*et al.*, 1987), and to check the performance of CCA (ter Braak, 1986). The option ‘detrrending-by-segments’ was selected, and rare (infrequent) taxa were downweighted to avoid overestimation of gradient lengths.

CCA (ter Braak, 1986) was used to relate the compositional variation to the environmental variables. The significance of the environmental variables was tested by a Monte Carlo permutation test (ter Braak & Šmilauer, 1998). We also examined intersite correlation between axes and variables. The relationship between variables was checked by Pearson’s correlation. If two variables are uncorrelated one would expect them to appear as two orthogonal vectors in the CCA-biplot. This may occur if they represent variation scaled at different spatial extents (Vetaas, 1993).

In CCA, interspecies distance and biplot scaling options were selected, and species only present in one or two plots were omitted, although some of them (*Quercus ilex* and *Tetraclinis articulata*) were made passive species, which have no influence on the ordination results. *Calicotome intermedia* was also made passive because its abundance was used as an explanatory variable indicating disturbance (CALICO).

#### *Comparison of the main compositional gradients*

We used the procedure outlined by Vetaas (1997) to evaluate the hypothesis that a species’ position (i.e. optimum in CCA) on the topoclimate gradient is reflected in its position on the longitudinal climate gradient, and vice versa. The order of species along each constrained gradient was determined by two different CCAs: one of them was constrained by LONGI only, and the other by RADIN only. To obtain the broad-scale compositional gradient without interference from the local-scale compositional gradient, the variation related to RADIN (local-scale factor) was removed by partial CCA (Jongman *et al.*, 1987; Vetaas, 1997). To produce the local-scale gradient without interference from the broad-scale gradient, the variance related to LONGI was partialled out.

The species scores along these constrained CCA-axes were then compared by Spearman’s rank correlation. If the order of the species along the axes is similar, it may imply that species with affinity to eastern (mesic) distribution also appear on northern slopes (low RADIN). This may indicate that the broad-scale compositional

**Table 1** DCA- and CCA-ordination results on compositional data and environmental variables. Significant intersite correlation coefficients ( $R$ ) are shown ( $R > 30.6$ ,  $P < 0.001$ ;  $R > 24.2$ ,  $P < 0.01$ ;  $R < 18.5$ ,  $NS = P > 0.05$ ;  $n = 113$ ). All eigenvalues and coefficients  $\times 100$ . Abbreviations: % Var SER = percentage variance of species–environment relationship explained.

| Axes                   | DCA-ordination |     |    | CCA-ordination |     |    |
|------------------------|----------------|-----|----|----------------|-----|----|
|                        | 1              | 2   | 3  | 1              | 2   | 3  |
| Eigenvalues            | 29             | 15  | 10 | 27             | 16  | 11 |
| % Var SER              | 43             | 22  | 0  | 45             | 27  | 18 |
| Inter-set correlations |                |     |    |                |     |    |
| LONGI                  | 55             | 55  | NS | 55             | 69  | NS |
| RADIN                  | 64             | -42 | NS | 67             | -38 | NS |
| ELEVA                  | NS             | 66  | 22 | NS             | 68  | NS |
| CALICO                 | NS             | NS  | 61 | NS             | 20  | 76 |

Environmental variables: LONGI = longitude; RADIN = radiation index; ELEVA = elevation; CALICO = disturbance index (see text).

gradient is mimicked by the local-scale gradient at each site, and that similar operational factors act at these two scales. This prediction is assumed to be most correct for species with a relatively wide spatial distribution and less accurate for infrequent taxa with a limited longitudinal range. However, it is still possible to relate their optima along both gradients to their biogeographical affinities, i.e. their chorological types (see below).

#### Biogeographical analysis

We used rank correlation to elucidate whether the different chorotypes (defined as number of species per plot) confirm the hypothesis of macro- and micropattern relationships. Based on the relation between micro (topoclimate) and macro-climate, we conjectured that species mainly found in North Africa (e.g. Mediterraneo–Saharo–Arabian species) should appear on southern aspects (high RADIN) in the arid west of the Cartagena range, whereas species distributed throughout more humid areas of the Mediterranean Basin (mainly Mediterranean or western Mediterranean taxa) should have affinities to northern slopes in the east. The chorotypes analysed were: south-east Iberian endemic (SEIB), Iberian endemic (IB), Ibero–Maghribian (and/or south-western Mediterranean, IMA), western Mediterranean (WMED), Mediterranean (MED), Mediterraneo–Macaronesian (M-MAC)

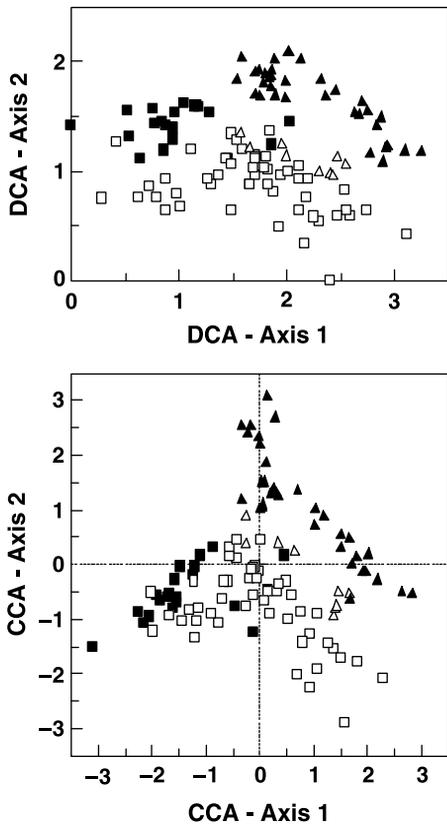
and Mediterraneo–Saharo–Arabian (M-SAH). The three first chorotypes (cf. above) are considered endemic (cf. Ojeda *et al.*, 1996; Le Houérou, 2001). Those restricted to the Mediterranean Region are ranked hierarchically. The distribution of all taxa is presented in Appendix 1. Chorological attributes were obtained mainly from standard floras (Valdés *et al.*, 1987; de Bolòs & Vigo, 1984–96, and Castroviejo, 1986–2001).

All ordinations and the Monte Carlo permutation tests were performed using CANOCO 4 (ter Braak & Šmilauer, 1998). This program was also used to obtain the associated correlations and ordination diagnostics. For standard and rank correlations, the program SPSS version 9.0.1. (Anonymous, 1999) was used.

## RESULTS

### Compositional data

The lengths of the two first species-axes in DCA-ordination are 3.3 and 2.1 SD-units long, respectively. The eigenvalues of the first three CCA-axes are 0.27, 0.16 and 0.11. The overall ordination results in DCA and CCA are similar (Table 1; Fig. 2), which implies that the variables selected are good predictors of the compositional variation. The Monte Carlo permutation test in CCA confirmed that all variables are significant ( $P = 0.001$ , 999 permutations). Both DCA and



**Fig. 2** DCA and CCA diagrams for samples (axes 1 and 2). Site 1 = ■; Site 2 = □; Site 3 = △; Site 4 = ▲. Samples scores are the weighted average of species scores.

CCA suggest that RADIN and LONGI are the most important variables in this analysis, because they are correlated most strongly to the first two axes (Table 1). In both ordinations, ELEVA is most strongly correlated to axis 2, whereas CALICO is mainly related to axis 3.

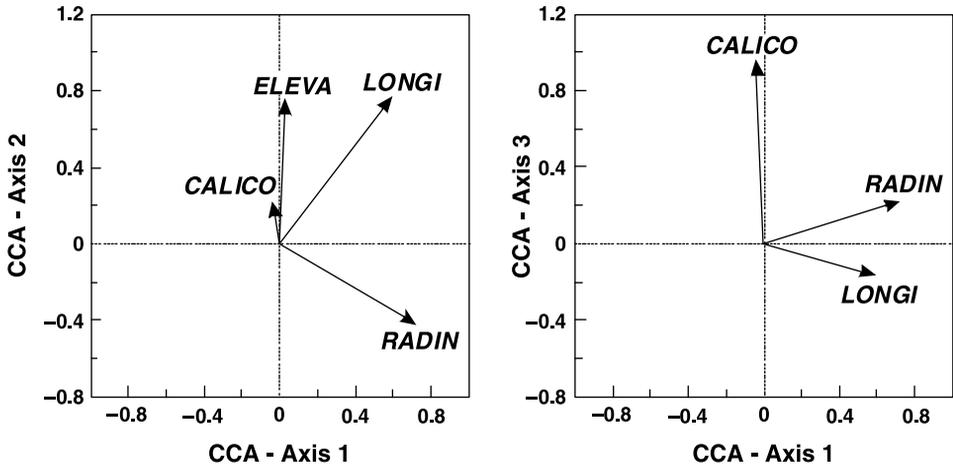
The correlation between variables indicated linear independence between all of them, except for LONGI and ELEVA ( $r = 0.50$ ;  $P < 0.001$ ). Both RADIN and LONGI are correlated to the two first ordination axes (Table 1), and their respective vectors are orthogonal to each other in the CCA-ordination plane (Fig. 3a). The disturbance variable (CALICO) explains a compositional variation independent of LONGI and RADIN (Fig. 3b).

#### Variation on the broad scale

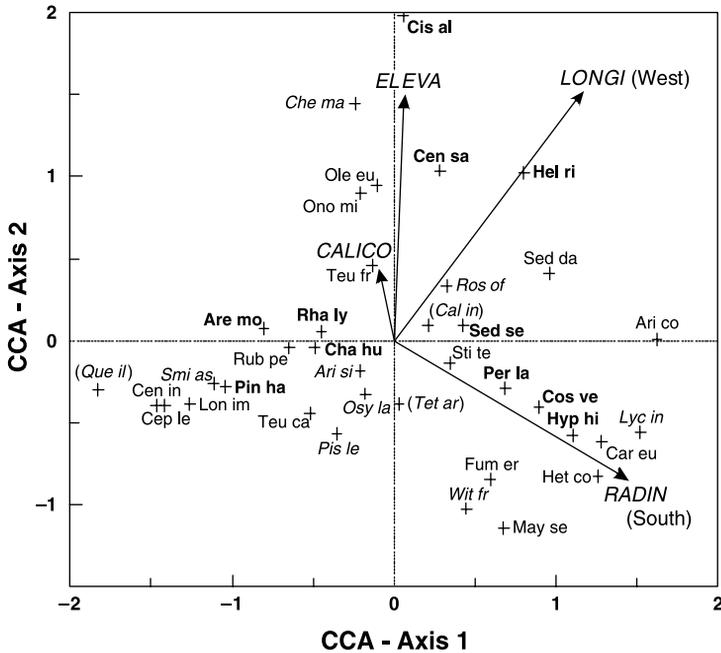
The main compositional variation along the Cartagena range is shown in Fig. 4. Some species were only observed in the humid east (they have negative scores on the first two CCA-axes). Among them, *Centaurea intybacea* Lam. and the infrequent *Quercus ilex* are exclusively restricted to S1. *Cephalaria leucantha* (L.) Roemer & Schultes and the climbers *Lonicera implexa* Aiton ssp. *implexa* and *Smilax aspera* L. are common at this site, and scarce in S2. Many species appear along the whole mountain range, though some of them are more frequent in the east (e.g. *Pinus halepensis*, the dwarf-palm *Chamaerops humilis* L., *Arenaria montana* L. ssp. *intricata* (Dufour) Pau), and others in the west (*Olea europaea* L., *Ononis minutissima* L., *Teucrium freynii* Reverchon ex Willk.). Species with the highest scores on CCA-axis 1, such as *Aristida coerulescens* Desf. and the stem succulent *Caralluma europaea* (Guss.) N.E. Br., are absent in S1. Others, such as *Helianthemum rigualii* Alcaraz, Peinado & Martínez-Parras and *Cheilanthes maderensis* Lowe (high scores on CCA-axis 2), were only observed in S4.

#### Variation at the local scale

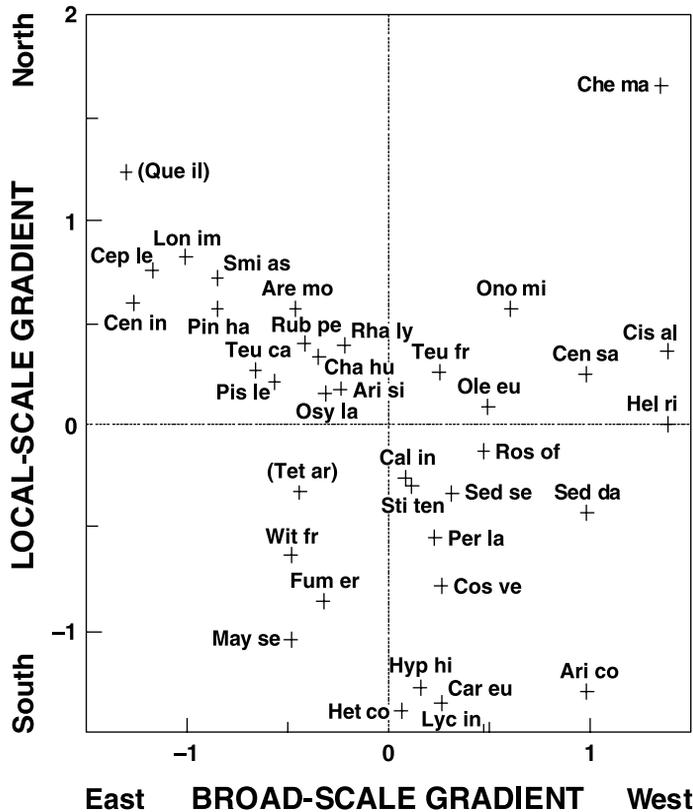
Some species with negative scores on CCA-axis 1 (e.g. *Cephalaria leucantha*, *Smilax aspera* and *Lonicera implexa*) are exclusively confined to north-facing slopes (Fig. 4). Others, such as *Chamaerops humilis* and *Rhamnus lycioides* L., are found mainly on northern hillsides. Some taxa (e.g. *Arisarum simurhinum* Durieu and *Osyris lanceolata* Hochst. & Steud.) are frequent at all slope aspects, but in the east. *Olea europaea* is more frequent with intermediate RADIN, especially towards the west. *Cheilanthes maderensis*, *Cistus albidus* L. and *Centaurea saxicola* Lag. are common on northern aspects (S4). *Helianthemum rigualii* and *Sedum dashyphyllum* L. (positive scores on the first two CCA-axes) are frequent on all slope aspects, also in the west. Some taxa with positive scores on CCA-axis 1 and negative scores on CCA-axis 2 (e.g. *Periploca laevigata* Aiton, *Cosentinia vellea* (Aiton) Tod. and *Stipa tenacissima* L.) are more frequent on southern slopes, and others are restricted exclusively to these hillsides (e.g. *Caralluma europaea* and *Hyparrhenia hirta* (L.) Stapf).



**Fig. 3** Vectors representing environmental variables in (a) CCA-ordination plane (axes 1 and 2), and (b) CCA-ordination plane (axes 1 and 3). LONGI = longitude; RADIN = radiation index; ELEV = elevation; CALICO = disturbance index (see text).



**Fig. 4** CCA biplot for species and environmental variables. Species with more than 30% of the variance explained by the first two axes are in bold, species with fits of 15–30% in normal letters, and with fits of 5–15% in italics. Full plant names are shown in Appendix 1; environmental variables as in Fig. 3.



**Fig. 5** Scatter-plot of the rank order of species along the geographical and local-scale gradients. Abbreviations as in Fig. 4, and full plant names in Appendix 1.

### Correspondence between the main compositional gradients

LONGI and RADIN are both correlated to CCA-axis 1 (Table 1; Fig. 3b). This may indicate that both variables are related to the same compositional gradient although they seem to be independent variables (Fig. 3a).

The comparison between the species scores on statistically uncorrelated broad- and local-scale gradients confirms that a significant proportion of species have a similar rank order on both gradients ( $r_s = -0.29$ ;  $P < 0.003$ ). The overall relations between the species order on these gradients can be seen in Fig. 5 and Appendix 1. The plot shows that numerous species have a similar order on the gradients, which is indicated by the distance between the taxa and an imaginary line from the upper left to the lower right corner of the graph.

Among them are most M-MAC, several MED (e.g. *Lonicera implexa*), WMED (notably *Chamaerops humilis*) and M-SAH (e.g. *Aristida coerulescens*), whereas *Cheilanthes maderensis*, several SEIB endemics (e.g. *Centaurea saxicola* and *Helianthemum rigualii*), and some IMA such as *Maytenus senegalensis* (Lam.) Exell ssp. *europaeus* (Boiss.) Rivas-Martínez, have low similarity.

### Chorological data

The main chorological variation is summarized in Table 2. M-MAC is correlated negatively to LONGI, whereas SEIB, IMA and M-SAH are correlated positively (i.e. most species of the former group are restricted to the east, whereas the latter increase in number towards the west). MED, WMED and IB show no trend related to LONGI, together with total species richness.

**Table 2** Spearman's rank correlation coefficients ( $\times 100$ ) between the number of species per plot of each chorotype and environmental variables. Variables, significance and  $n$  as in Table 1.  $N$  = total species number

| Chorotype <sup>1</sup> | $N$ | LONGI | RADIN | ELEVA | CALICO |
|------------------------|-----|-------|-------|-------|--------|
| SEIB                   | 18  | 38    | -29   | 22    | 32     |
| IB                     | 6   | NS    | -20   | NS    | NS     |
| IMA                    | 15  | 19    | 30    | -28   | 60     |
| WMED                   | 23  | NS    | -45   | NS    | 29     |
| MED                    | 37  | NS    | -37   | NS    | 19     |
| M-MAC                  | 9   | -50   | -46   | -25   | -27    |
| M-SAH                  | 10  | 32    | 68    | NS    | NS     |
| Richness               | 124 | NS    | -30   | NS    | 39     |

<sup>1</sup> SEIB = South-east Iberian endemic; IB = Iberian endemic; IMA = Ibero-Maghribian and/or south-western Mediterranean; WMED = western Mediterranean; MED = Mediterranean; M-MAC = Mediterranean-Macaronesian; M-SAH = Mediterranean-Saharo-Arabian.

M-MAC, MED, WMED, IB, SEIB and also total richness are negatively correlated with RADIN (i.e. they tend to appear on northern slopes), whereas IMA and M-SAH are positively correlated. SEIB endemics also have a positive correlation with CALICO and ELEVA.

### The effect of disturbance

CALICO is correlated strongly to axis 3 in both DCA and CCA (Table 1; Fig. 3b), which may indicate a disturbance gradient. Species richness increases significantly with CALICO, together with the number of SEIB and IMA (Table 2). Sites with high positive scores on CCA-axis 3 have a mean density of *Calicotome intermedia* of c. 20 stems/100 m<sup>2</sup>, and intermediate values of RADIN and/or LONGI. *Thymelaea hirsuta* (L.) Endl, *Carlina hispanica* Lam. and *Helianthemum syriacum* (Jacq.) Dum.-Cours. have the highest scores on this axis. Other taxa associated with CALICO are *Eryngium campestre* L., *Convolvulus althaeoides* L. and *Teucrium pseudo-chamaepitidis* L. All of them have been related to disturbed sites in south-eastern Spain (cf. Esteve Chueca, 1973; Dargie, 1984).

## DISCUSSION

### Compositional variation and environmental factors

The overall ordination results in DCA and CCA indicate that major operational factors are

represented by the variables selected. Because both the broad- (LONGI) and local-scale (RADIN) factor-complexes are correlated to the same CCA- and DCA-ordination axes, they must relate to the same general trend in species-turnover. They have, at least in part, similar effects on species distribution, and explain why a significant proportion of species has a similar rank order on both gradients (Fig. 5). Thus there are local-scale patterns within the broad-scale pattern that mimic each other, which may be interpreted as a form of self-similarity (Vetaas, 1997).

This self-similar pattern may appear when water and/or temperature are the principal determinants of plant distribution (Vetaas, 1992, 1997). In SE Spain the main constraint seems to be water stress, as in other arid or semi-arid regions (Ezcurra *et al.*, 1987; Dargie & El Demerdash, 1991), but some species may be sensitive to temperature, especially to frosts (cf. Peinado *et al.*, 1992). The steep gradients induced by aspect and a strong insolation climate (Dargie, 1984) may be enhanced in the Cartagena area by the predominant winds (*levante* and *lebeche*). The combined effect of radiation and seasonal winds with different moisture content resembles the conditions that have been found to induce strong topoclimate gradients in the Red Sea Hills (north-eastern Sudan) (Vetaas, 1992).

Species with affinity to eastern (mesic) sites are associated with north-facing slopes, and species limited to southern hillsides have their optima in the west. Other taxa, with high correspondence

on the two scales, shift their habitat along the geographical gradient. Some of them (e.g. *Periploca laevigata* and *Cosentinia vellea*) are found on all slope aspects in the west, but only on southern slopes in the east. Others, such as *Chamaerops humilis* and *Arenaria montana* ssp. *intricata*, are restricted to humid aspects in the west, but are indifferent to aspect in the east. This change in habitat along the geographical gradient allows the species to remain under similar moisture and temperature conditions (i.e. to remain in a constant niche related to these factors) (Boyko, 1947; Loucks, 1962; Vetaas, 1992). This has sometimes been called 'habitat-constancy' (Walter & Walter, 1953; Miehe, 1989), but it is actually the real habitat that is changing, whereas the niche (abstract model) remains constant.

Some species have no correspondence between the two gradients, especially saxicolous plants (e.g. *Cheilanthes maderensis*). Many of them appear only on northern slopes, but in the west. They have been associated primarily with rock outcrops and aspect rather than with the general climate (Esteve Chueca, 1973). However, the increasing aridity towards the west inhibits the growth of most phanerophytes, implying a reduced soil development and the potential loss of this resource, resulting in persistent rock outcrops where only specialized (saxicolous) plants may survive.

### Chorological pattern

There is a good correspondence between the broad- and local-scale gradients with M-MAC, M-SAH and IMA (Table 2). The former group is restricted to the moist part of both gradients, whereas the two latter increase in number with increasing aridity. Dargie (1987) indicated that species' distribution along the topoclimate gradient was discontinuous in south-eastern Spain, and that species associated with northern slopes were more common at higher latitudes, and vice versa with southern species. He interpreted this as two separate geographical floras preserved at each end of the topoclimate gradient. We showed that M-MAC is linked to the northern (temperate) flora, but some taxa might have a tropical origin (Herrera, 1992), e.g. *Pistacia*. IMA is viewed as a steppic group with tropical or

subtropical affinities (Peinado *et al.*, 1992) and M-SAH as an archaic element of the Austro-Pan-African xerophytic flora (Le Houérou, 2001). A similar correspondence between broad- (latitudinal) and local-scale (topoclimate) gradients with northern (Mediterraneo–Euro–Siberian) and southern (Saharo–Arabian) species has been detected in Israel (Nevo *et al.*, 1999). A variation in the number of Mediterranean (Holarctic) and Sahelo–Sudanian (African) species related to latitudinal climate gradients has also been observed in the Sahara (Le Houérou, 2001). Analogous patterns were found with Boreal and Sonoran species in the White Mountains (California–Nevada) (Morefield, 1992).

MED and WMED are associated with northern slopes (Table 2), which supports the statement by Dargie (1987), but they have no significant trend along the geographical gradient. This may be because they are heterogeneous groups with complex mixtures of taxa of different origins and affinities (cf. Herrera, 1992). Thus there are old, pre-Mediterranean taxa such as *Pinus*, *Rhamnus*, *Quercus* and *Lonicera* that have been associated with the temperate flora (Raven, 1973), and more recent lineages (e.g. some Labiatae and Cistaceae) evolved presumably after the initiation of the Mediterranean climate (Pliocene) (Herrera, 1992; Cowling *et al.*, 1996). It seems that at least these old taxa also have a good correspondence between the two gradients (Appendix 1) and that they are replaced by the new ones on more arid northern slopes, which may explain the lack of broad-scale pattern.

Several of the local (SEIB) endemics are saxicolous. This clarifies why this group does not correspond on the broad- and local-scale gradients. They are edaphic-specialists, as in other Mediterranean-climate regions (Cowling *et al.*, 1996; Cowling & Lombard, 2002), with affinity to rock outcrops on northern slopes, particularly at high altitude (Table 2). This agrees with the idea that a high level of endemism is favoured by low rates of competitive displacement (Huston, 1994) and isolation at mountain peaks (Vetaas & Grytnes, 2002).

### Variation in total species richness

There is a significant decrease in species richness with high radiation in addition to the

compositional variation along the topoclimate gradient. This has also been found in central Murcia (Dargie, 1984), and is consistent with a common trend of increasing richness with increasing moisture availability (MacArthur, 1972; Pausas & Austin, 2001). Thus we expected an increase along the longitudinal gradient from west (dry) to east (moist), but this was not statistically significant. This may be due to the correspondence between high richness and disturbance (cf. Dargie, 1984), which both appear in the middle of the broad-scale gradient, while the closed forests in the east have lower richness than open woodlands and *espinares*, as in other Mediterranean areas (cf. Cowling *et al.*, 1996).

Although the species richness gradient is not repeated at different scales, the compositional gradient and the distribution of chorotypes show that the broad-scale gradient is, to some extent, mimicked at a local scale, which is important for the diversity.

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**Appendix I** Acronyms, chorological attributes (distribution) and ordination scores of species along the statistically uncorrelated (A) broad- and (B) local-scale CCA-axes

| Acron. | Species  | Distribution <sup>1</sup> | Code <sup>2</sup> | A    | B    |
|--------|--|---------------------------|-------------------|------|------|
|        | <i>Anthyllis cytisoides</i> L. <sup>3</sup>                          | WMED                      | 5                 | —    | —    |
|        | <i>Antirrhinum barrelieri</i> Boreau <sup>3</sup>                    | IMA                       | 3                 | —    | —    |
| Are mo | <i>Arenaria montana</i> L. ssp. <i>intricata</i> (Dufour) Pau        | IB                        | 2                 | -0.5 | 0.6  |
|        | <i>Argyrolobium zanonii</i> (Turra) P.W. Ball ssp. <i>zanonii</i>    | MED                       | 6                 | 0.4  | -0.7 |
| Ari si | <i>Arisarum simurrhinum</i> Durieu                                   | WMED-MAC                  | 7                 | -0.2 | 0.2  |
| Ari co | <i>Aristida coerulescens</i> Desf.                                   | M-SAH                     | 4                 | 1.0  | -1.3 |
|        | <i>Artemisia barrelieri</i> Besser                                   | IB                        | 2                 | 1.0  | -0.8 |
|        | <i>Asparagus albus</i> L.  | WMED                      | 5                 | -0.1 | -0.1 |
|        | <i>Asparagus horridus</i> L. fil.                                    | MED                       | 6                 | 0.1  | -0.3 |
|        | <i>Asperula aristata</i> L. fil. ssp. <i>scabra</i> (C. Presl) Nyman | MED                       | 6                 | 0.6  | -0.3 |
|        | <i>Asphodelus ramosus</i> L.   | MED                       | 6                 | -0.5 | -0.2 |
|        | <i>Asplenium petrarchae</i> (Guérin) DC. <sup>3</sup>                | MED                       | 6                 | —    | —    |
|        | <i>Asteriscus maritimus</i> (L.) Less.                               | MED                       | 6                 | 0.7  | -0.8 |
|        | <i>Atractylis humilis</i> L. ssp. <i>humilis</i>                     | WMED                      | 5                 | 0.3  | 0.2  |
|        | <i>Avenula murcica</i> J. Holub                                      | SEIB                      | 1                 | 0.2  | 0.2  |
|        | <i>Ballota hirsuta</i> Bentham                                       | IMA                       | 3                 | 0.0  | 0.0  |
|        | <i>Bituminaria bituminosa</i> (L.) C.H. Stirt.                       | M-MAC                     | 7                 | -0.8 | -1.2 |
|        | <i>Brachypodium retusum</i> (Pers.) Beauv.                           | MED                       | 6                 | -0.1 | 0.1  |
|        | <i>Bupleurum fruticosum</i> L.                                       | WMED                      | 5                 | -0.1 | 0.5  |
| Cal in | <i>Calicotome intermedia</i> C. Presl                                | IMA                       | 3                 | 0.1  | -0.3 |
| Car eu | <i>Caralluma europaea</i> (Guss.) N.E. Br.                           | M-SAH                     | 4                 | 0.3  | -1.3 |
|        | <i>Carex halleriana</i> Asso   | MED                       | 6                 | -0.2 | 0.6  |
|        | <i>Carlina hispanica</i> Lam.  | MED                       | 6                 | 0.4  | 0.3  |
| Cen in | <i>Centaurea intybacea</i> Lam.                                      | WMED                      | 5                 | -1.3 | 0.6  |
| Cen sa | <i>Centaurea saxicola</i> Lag.                                       | SEIB                      | 1                 | 1.0  | 0.3  |
| Cep le | <i>Cephalaria leucantha</i> (L.) Roemer & Schultes                   | MED                       | 6                 | -1.2 | 0.8  |
|        | <i>Ceterach officinarum</i> Willd. <sup>3</sup>                      | HOL                       | 8                 | —    | —    |
| Cha hu | <i>Chamaerops humilis</i> L.   | WMED                      | 5                 | -0.3 | 0.3  |
| Che ma | <i>Cheilanthes maderensis</i> Lowe                                   | WMED-MAC                  | 7                 | 1.4  | 1.7  |
| Cis al | <i>Cistus albidus</i> L.   | WMED                      | 5                 | 1.4  | 0.4  |
|        | <i>Cistus monspeliensis</i> L.                                       | M-MAC                     | 7                 | -1.1 | 0.5  |
|        | <i>Clematis cirrhosa</i> L.  | MED                       | 6                 | -0.8 | 1.2  |
|        | <i>Clematis flammula</i> L.  | M-MAC                     | 7                 | -1.3 | 0.6  |
|        | <i>Convolvulus althaeoides</i> L.                                    | MED                       | 6                 | -0.2 | -0.2 |
|        | <i>Convolvulus lanuginosus</i> Desr.                                 | WMED                      | 5                 | 0.6  | 0.0  |
|        | <i>Coris monspeliensis</i> L. <sup>3</sup>                           | MED                       | 6                 | —    | —    |
|        | <i>Coronilla juncea</i> L.   | MED                       | 6                 | -0.1 | 0.4  |
| Cos ve | <i>Cosentinia vellea</i> (Aiton) Tod.                                | M-SAH (CA)                | 4                 | 0.3  | -0.8 |
|        | <i>Dactylis glomerata</i> L. ssp. <i>hispanica</i> (Roth) Nyman      | MED                       | 6                 | 0.1  | 0.2  |
|        | <i>Daphne gnidium</i> L.   | M-MAC                     | 7                 | -0.4 | 0.7  |
|        | <i>Dianthus broteri</i> Boiss. & Reut.                               | IB                        | 2                 | -1.0 | -0.6 |
|        | <i>Dorycnium pentaphyllum</i> Scop. ssp. <i>pentaphyllum</i>         | MED                       | 6                 | -1.2 | 0.6  |
|        | <i>Elaeoselinum tenuifolium</i> (Lag.) Lange                         | IB                        | 2                 | -0.3 | -0.1 |
|        | <i>Eryngium campestre</i> L.   | HOL                       | 8                 | -0.1 | 0.1  |
|        | <i>Euphorbia squamigera</i> Loisel. <sup>3</sup>                     | WMED                      | 5                 | —    | —    |
|        | <i>Fagonia cretica</i> L.  | M-SAH                     | 4                 | -0.1 | -0.3 |
| Fum er | <i>Fumana ericoides</i> (Cav.) Gand.                                 | IMA (BA)                  | 3                 | -0.3 | -0.9 |
|        | <i>Fumana laevipes</i> (L.) Spach                                    | MED                       | 6                 | 0.2  | -0.2 |
|        | <i>Fumana thymifolia</i> (L.) Spach ex Webb                          | MED                       | 6                 | 0.3  | 0.0  |

## Appendix I continued.

| Acron. | Species  | Distribution <sup>1</sup> | Code <sup>2</sup> | A    | B    |
|--------|--|---------------------------|-------------------|------|------|
|        | <i>Genista jimenezii</i> Pau   | SEIB                      | 1                 | 0.7  | 0.6  |
|        | <i>Genista umbellata</i> (L'Hér.) Poir. ssp. <i>umbellata</i>  | IMA                       | 3                 | 0.2  | -0.4 |
|        | <i>Globularia alypum</i> L. <sup>3</sup>   | MED                       | 6                 | —    | —    |
|        | <i>Haplophyllum linifolium</i> (L.) G. Don fil. ssp. <i>rosmarinifolium</i> (Pers.) O. Bolòs & Vigo <sup>3</sup> | IB                        | 2                 | —    | —    |
|        | <i>Helianthemum almeriense</i> Pau   | SEIB                      | 1                 | -0.3 | -0.4 |
| Hel ri | <i>Helianthemum rigualii</i> Alcaraz, Peinado & Martínez-Parras  | SEIB                      | 1                 | 1.4  | 0.0  |
|        | <i>Helianthemum syriacum</i> (Jacq.) Dum.-Cours.   | MED                       | 6                 | -0.4 | -0.3 |
|        | <i>Helichrysum decumbens</i> (Lag.) Camb.  | SEIB                      | 1                 | 0.1  | 0.2  |
|        | <i>Helictotrichon filifolium</i> (Lag.) Henrard  | WMED                      | 5                 | -0.1 | 0.3  |
| Het co | <i>Heteropogon contortus</i> (L.) Beauv. ex Roemer & Schultes  | M-SAH                     | 4                 | 0.1  | -1.4 |
| Hyp hi | <i>Hyparrhenia hirta</i> (L.) Stapf  | M-MAC-PT                  | 8                 | 0.2  | -1.3 |
|        | <i>Jasonia saxatilis</i> (Lam.) Guss <sup>3</sup>  | WMED                      | 5                 | —    | —    |
|        | <i>Lafuentea rotundifolia</i> Lag. <sup>3</sup>  | SEIB                      | 1                 | —    | —    |
|        | <i>Lapiedra martinezii</i> Lag.  | IMA                       | 3                 | -0.1 | 0.2  |
|        | <i>Launaea arborescens</i> (Batt.) Murb. <sup>3</sup>  | M-SAH (CA)                | 4                 | —    | —    |
|        | <i>Launaea lanifera</i> Pau  | M-SAH                     | 4                 | 0.2  | -1.4 |
|        | <i>Lavandula dentata</i> L.  | M-MAC                     | 7                 | -0.2 | 0.1  |
|        | <i>Lavandula multifida</i> L.  | M-SAH                     | 4                 | 0.8  | -1.4 |
|        | <i>Lavatera maritima</i> Gouan <sup>3</sup>  | WMED                      | 5                 | —    | —    |
|        | <i>Limonium carthaginense</i> (Rouy) Hubb. & Sandwith <sup>3</sup>   | SEIB                      | 1                 | —    | —    |
|        | <i>Linum suffruticosum</i> L. <sup>3</sup>   | IMA                       | 3                 | —    | —    |
|        | <i>Lithodora fruticosa</i> (L.) Griseb.  | WMED                      | 5                 | -0.7 | 0.3  |
|        | <i>Lobularia maritima</i> (L.) Desv.   | MED                       | 6                 | 0.2  | -0.7 |
| Lon im | <i>Lonicera implexa</i> Aiton ssp. <i>implexa</i>  | MED                       | 6                 | -1.0 | 0.8  |
| Lyc in | <i>Lycium intricatum</i> Boiss.  | MED                       | 6                 | 0.5  | -1.5 |
| May se | <i>Maytenus senegalensis</i> (Lam.) Exell ssp. <i>europaeus</i> (Boiss.) Rivas-Martínez                          | IMA                       | 3                 | -0.5 | -1.0 |
|        | <i>Melica minuta</i> L.  | MED                       | 6                 | 0.0  | 0.5  |
| Ole eu | <i>Olea europaea</i> L.  | M-MAC-PT-SA               | 8                 | 0.5  | 0.1  |
| Ono mi | <i>Ononis minutissima</i> L.   | WMED                      | 5                 | 0.6  | 0.6  |
| Osyl   | <i>Osyris lanceolata</i> Hochst. & Steud.  | IMA-SA                    | 8                 | -0.3 | 0.2  |
|        | <i>Paronychia suffruticosa</i> (L.) DC. ssp. <i>suffruticosa</i>   | IB                        | 2                 | 0.1  | 0.0  |
| Per la | <i>Periploca laevigata</i> Aiton   | M-SAH (CA)                | 4                 | 0.2  | -0.6 |
|        | <i>Phagnalon rupestre</i> (L.) DC.   | MED                       | 6                 | 0.6  | 0.1  |
|        | <i>Phagnalon saxatile</i> (L.) Cass.   | WMED                      | 5                 | 0.1  | -0.1 |
|        | <i>Phlomis lychnitis</i> L.  | WMED                      | 5                 | 1.0  | -0.1 |
| Pin ha | <i>Pinus halepensis</i> Miller   | MED                       | 6                 | -0.9 | 0.6  |
|        | <i>Piptatherum coerulescens</i> (Desf.) Beauv.   | MED                       | 6                 | 0.4  | -0.1 |
| Pis le | <i>Pistacia lentiscus</i> L.   | M-MAC                     | 7                 | -0.6 | 0.2  |
|        | <i>Polygala rupestris</i> Pourr.   | WMED                      | 5                 | -0.2 | 0.2  |
|        | <i>Quercus coccifera</i> L.  | MED                       | 6                 | -0.4 | 0.8  |
| Que il | <i>Quercus ilex</i> L. <sup>4</sup>  | MED                       | 6                 | -1.3 | 1.2  |
|        | <i>Rhamnus alaternus</i> L.  | MED                       | 6                 | -0.5 | 0.9  |
| Rha ly | <i>Rhamnus lycioides</i> L.  | WMED                      | 5                 | -0.2 | 0.4  |
| Ros of | <i>Rosmarinus officinalis</i> L.   | MED                       | 6                 | 0.5  | -0.1 |
| Rub pe | <i>Rubia peregrina</i> L. ssp. <i>longifolia</i> (Poiret) O. Bolòs   | MED                       | 6                 | -0.4 | 0.4  |
|        | <i>Ruta angustifolia</i> Pers.   | WMED                      | 5                 | -0.6 | 0.0  |
|        | <i>Salsola oppositifolia</i> Desf. <sup>3</sup>  | M-SAH (CA)                | 4                 | —    | —    |
|        | <i>Satureja obovata</i> Lag.   | SEIB                      | 1                 | 0.1  | 0.0  |

## Appendix I continued.

| Acron. | Species  | Distribution <sup>1</sup> | Code <sup>2</sup> | A    | B    |
|--------|--|---------------------------|-------------------|------|------|
|        | <i>Scorzonera angustifolia</i> L.  | IMA                       | 3                 | 0.2  | 0.1  |
|        | <i>Scrophularia sciophila</i> Willk.   | SEIB                      | 1                 | -1.3 | 0.7  |
| Sed da | <i>Sedum dasyphyllum</i> L.  | MED                       | 6                 | 1.0  | -0.4 |
| Sed se | <i>Sedum sediforme</i> (Jacq.) Pau   | MED                       | 6                 | 0.3  | -0.3 |
|        | <i>Senecio malacitanus</i> Huter <sup>3</sup>  | IMA                       | 3                 | —    | —    |
|        | <i>Serratula flavescens</i> (L.) Poir. ssp. <i>mucronata</i> (Desf.) Cantó & Costa <sup>3</sup>        | IMA                       | 3                 | —    | —    |
|        | <i>Sideritis ibanyezii</i> Pau <sup>3</sup>  | SEIB                      | 1                 | —    | —    |
|        | <i>Sideritis pusilla</i> (Lange) Pau ssp. <i>carthaginensis</i> (Font Quer) Alcaraz <i>et al.</i>      | SEIB                      | 1                 | -0.7 | 0.5  |
| Smi as | <i>Smilax aspera</i> L.  | M-MAC-PT                  | 8                 | -0.9 | 0.7  |
|        | <i>Stipa offneri</i> Breistr.  | WMED                      | 5                 | 1.1  | 0.9  |
|        | <i>Stipa parviflora</i> Desf.  | WMED                      | 5                 | 0.3  | -1.3 |
| Sti te | <i>Stipa tenacissima</i> L.  | IMA (BA)                  | 3                 | 0.1  | -0.3 |
| Tet ar | <i>Tetraclinis articulata</i> (Vahl) Masters <sup>4</sup>  | IMA (CC)                  | 3                 | -0.4 | -0.3 |
|        | <i>Teucrium capitatum</i> L. ssp. <i>gracillimum</i> (Rouy) Valdés-Bermejo                             | SEIB                      | 1                 | 0.5  | 0.2  |
|        | <i>Teucrium carolipau</i> C. Vicioso ex Pau ssp. <i>fontqueri</i> (Sennen) Rivas-Martínez <sup>±</sup> | SEIB                      | 1                 | —    | —    |
| Teu c. | <i>Teucrium carthaginense</i> Lange  | SEIB                      | 1                 | -0.7 | 0.3  |
| Teu fr | <i>Teucrium freynii</i> Reverchon ex Willk.  | SEIB                      | 1                 | 0.3  | 0.3  |
|        | <i>Teucrium murcicum</i> Sennen  | SEIB                      | 1                 | -1.1 | -0.1 |
|        | <i>Teucrium pseudo-chamaepitis</i> L.  | WMED                      | 5                 | -0.2 | -0.2 |
|        | <i>Thesium humifusum</i> DC.   | MED                       | 6                 | 1.0  | 0.7  |
|        | <i>Thymelaea argentata</i> (Lam.) Pau  | IMA                       | 3                 | 0.7  | 0.3  |
|        | <i>Thymelaea hirsuta</i> (L.) Endl.  | MED                       | 6                 | -0.1 | -0.1 |
|        | <i>Thymus hyemalis</i> Lange   | SEIB                      | 1                 | 0.1  | -0.1 |
|        | <i>Umbilicus gaditanus</i> Boiss.  | WMED-MAC                  | 7                 | 0.0  | 0.9  |
|        | <i>Urginea maritima</i> (L.) Baker   | MED                       | 6                 | 0.2  | 0.0  |
|        | <i>Viola arborescens</i> L.  | WMED                      | 5                 | -0.2 | 0.3  |
| Wit fr | <i>Withania frutescens</i> (L.) Pauquy   | IMA (BA)                  | 3                 | -0.5 | -0.6 |

<sup>1</sup>SEIB = South-east Iberian endemic; IB = Iberian endemic; IMA = Ibero-Magribian and/or south-western Mediterranean; WMED = western Mediterranean; MED = Mediterranean; M-MAC = Mediterraneo-Macaronesian; M-SAH = Mediterraneo-Saharo-Arabian; HOL = Holarctic; PT = Palaeotropical; SA = South African. In brackets, locations that hardly exceed the region considered for chorological analysis (BA = Balearic isles, CA = Canary Islands, CC = Cyrenaica and Cyprus).

<sup>2</sup>Codes for the chorotypes analysed: 1 = SEIB, 2 = IB, 3 = IMA, 4 = M-SAH, 5 = WMED, 6 = MED, 7 = M-MAC. Other types not analysed: 8 = HOL, PT and/or SA.

<sup>3</sup>Infrequent taxa, omitted in constrained ordinations.

<sup>4</sup>Passive species.