



Endemic flora biodiversity in the south of the Iberian Peninsula: altitudinal distribution, life forms and dispersal modes

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Abstract. The south of the Iberian Peninsula, with an altitudinal range varying from sea level to 3482 m and annual average rainfall ranging from 206 to 2223 mm, has 516 vascular endemic species or subspecies, that is, an endemicity rate of 13%. This survey deals with parameters such as species richness, originality, life forms and dispersal modes of these plants, in relation to altitudinal and rainfall gradients. Although most of the endemic plants occur between 600 and 1400 m a.s.l. and in the range of 600–1000 mm annual average rainfall, floristic originality (rate of endemic taxa per area unit) increases exponentially with altitude. The biological spectrum of this endemic flora does not follow the usual patterns observed either in local floras in the south of the Iberian Peninsula or in other regions of the Mediterranean Basin. Chamaephytes (46.08%) and hemicryptophytes (31.37%) are very abundant, whereas therophytes (11.96%) and phanerophytes (0.98%) are comparatively rare. There is a statistically significant correlation between life form and both altitudinal and rainfall gradients. Chamaephytes reach their highest density rates within 1400–2000 m a.s.l., but these records tend to decrease as rainfall rates increase. Abundance of hemicryptophytes is directly dependent on rainfall rates and inversely dependent on temperature. The altitudinal distribution pattern of therophytes is opposite to that of hemicryptophytes, but there is no clear correlation as far as rainfall gradient is concerned. Considering both the endemic plants as a whole and each of the life form groups, the relationships between the dispersal modes used and the altitudinal and rainfall gradients are analysed. Up to 44.51% of the endemic plants do not present evident adaptations to promote the dispersion of their diaspores. However, only in the group of therophytes, whose occurrence is positively related to areas of minor altitude, does this difficulty of dispersion play a significant role in the maintenance of stenochory.

Introduction

The south of the Iberian Peninsula presents a great floristic richness. Estimates are that ca. 4000 vascular plant species or subspecies occur in an area of less than 88 000 km² (Hernández Bermejo and Clemente 1994). The area represents one of the most outstanding biodiversity hotspots of the Mediterranean Basin (Médail and Quézel 1997, 1999). This floristic richness is the consequence of not only high local diversity (a large number of species sharing a common territory), but also of high regional diversity

(environmental conditions and landscapes changing dramatically from one spot to another) (Blondel and Aronson 1995). The flora of the territory shows a high endemism rate which in some places reaches up to 36% (Blanca et al. 2002).

In recent years, this peculiar endemic flora has been the subject of a great number of scientific studies on different aspects. Since the detailed analysis of plant distribution provides objective and very useful criteria to later assess and manage these areas (Gómez Campo and Malato Beliz 1985), many of these surveys tend to concentrate on taxa distribution (see, e.g., Blanca and Valle (1996) and references included). Other recent surveys deal with biology, ecological behaviour, vulnerability and preservation problems of some of these endemic plants (Gómez Campo 1987; Hernández Bermejo and Clemente 1994; Blanca et al. 1999, 2000). There are also a number of biogeographical and preservationist studies which aim at both defining floristic territories and determining priorities for preservation policies (García-Barros et al. 2002). Up to now, however, the floristic originality, life forms and dispersal modes of this endemic flora, in relation to altitudinal gradient, had not been studied.

Generally speaking, most of the surveys dealing with the altitudinal gradient have tended to concentrate on species richness (Lieberman et al. 1996; Vásquez and Givnish 1998; Austrheim 2002, etc.), on the zonation of the diverse vegetation types (see, e.g., Frahm and Gradstein 1991), or on the variations of the floristic composition (see, e.g., Hemp 2002). Researchers, however, have paid little attention to the altitudinal distribution of the endemic plants (Kessler 2000). Some surveys, however, have revealed the relationships between geographical distribution patterns and ecological features such as life form and dispersal mode (Gentry 1988). These same characteristics either of local floras (Fitter and Peat 1994; Buide et al. 1998) or of particular taxonomical groups (Ricklefs and Renner 1994) have produced some studies, but the endemic floras have not been surveyed in a similar way up to now.

The study of these characteristics of the endemic flora, together with their relationship to ecological gradients, such as those of altitude and rainfall, will not only reveal general patterns, but also the peculiarities and differences between the groups of endemic plants. In this respect, the aims of this survey are: (1) to estimate the floristic originality (number of endemic taxa per area unit) of the flora in the south of the Iberian Peninsula and its relationship, if any, with the altitudinal gradient, (2) to analyse the spectrum of life forms of this endemic flora in relation to altitude and rainfall rate, and, finally, (3) to analyse the dispersal modes of this flora in relation to altitude and rainfall gradients. Hopefully, this knowledge will lead to better criteria for the implementation of preservation policies.

Material and methods

Study area

The study area, located between 36°00' and 38°45' north latitude and 1°35' and 7°35' west longitude, comprises 87,597 km². It encompasses the south of the

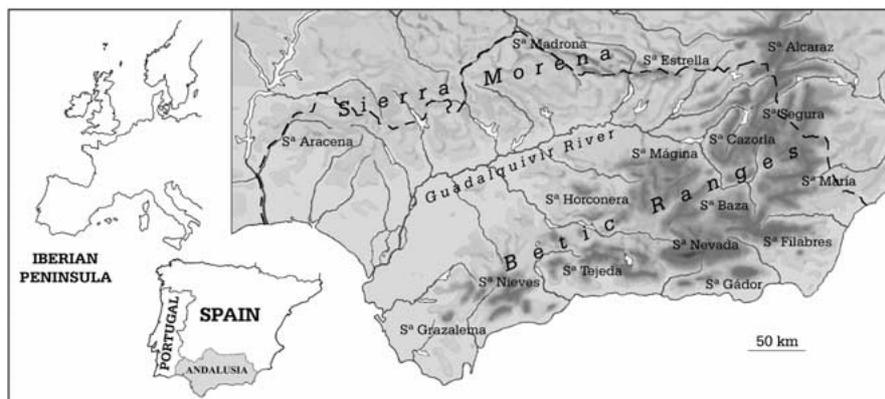


Figure 1. Location and morphostructural units of the study area.

Iberian Peninsula and corresponds to the administrative territory of Andalusia (Figure 1). One of the most remarkable features of the study area is its enormous orographical, geological, edaphic and climatic diversity, which gives rise to its floristic, phytocoenotical and biogeographical diversity (Rivas-Martínez et al. 1997). Three large morphostructural units can be distinguished: the Betic ranges, Sierra Morena and the depression of the Guadalquivir river.

The mountainous rim of Sierra Morena represents the southern slope of the Iberian Meseta and is, at the same time, the northern border of the study area. Altitude decreases from east to west, ranging from 1300 m a.s.l., in Sierra Madrona or Sierra de la Estrella, to 200 m at the western limits, where Sierra de Aracena constitutes an area of high land. This unit is made up of siliceous lithological materials, such as slates, granites and quartzites, with occasional Palaeozoic limestone outcrops.

The Betic ranges constitute the southern fringe of the study area. The altitudinal range is higher, ranging from sea level to the 3482 m of Mount Mulhacén in Sierra Nevada, the highest peak in the Iberian Peninsula. Although no other mountain chain can rival the impressive height and extension of Sierra Nevada, there are many ranges over 2000 m altitude, such as the ranges of Cazorra, Mágina, Baza, María, Filabres, Gádor, Tejada, and so forth. Other ranges, such as Sierra de Grazalema or Sierra de las Nieves, do not reach this height, but are of great floristic value. Geological substrates are mostly limestones and dolomites, with extensive outcrops of siliceous materials, such as mica-schists and phyllites. These ranges also comprise inner depressions with clayey or marly soils, sometimes rich in salts.

The great depression of the Guadalquivir River lies between the two former units, with altitudes ranging from sea level, in the marshlands of Doñana, to 300 m a.s.l. at its eastern boundary. Detrital and marly materials are very abundant here.

The whole study area has a Mediterranean macroclimate. In the area, five bioclimatic belts or thermotypes (Rivas-Martínez and Loidi 1999) can be

Table 1. Altitudinal range, area, number of endemic plants and floristic originality of the thermotypes in the south of the Iberian Peninsula. No. end.: number of endemic plants.

Thermotypes	Altitude (m)	Area (km ²)	Area rate	No. end.	No. end./area rate
Thermomediterranean	<600	33059.11	37.74	156	4.13
Mesomediterranean	600–1400	47039.59	53.70	236	4.39
Supramediterranean	1400–2000	6368.30	7.27	202	27.79
Oromediterranean	2000–2800	1077.44	1.23	158	128.46
Cryromediterranean	>2800	52.56	0.06	55	916.67

distinguished. The limits between these belts coincide with the distribution areas of many taxa and phytocoenoses. These thermotypes have been defined using the records of annual average temperature and highest and lowest temperatures of the coldest month, records which are clearly altitude-dependent. Table 1 shows the average altitudinal range and the area of the thermotypes in the study area. Annual average rainfall records vary from 206 mm in Almería to 2223 mm in Grazalema. According to rainfall intervals in mm, the following five ombrotypes can also be distinguished (Rivas-Martínez 1987): semiarid (200–350), dry (350–600), sub-humid (600–1000), humid (1000–1600) and hyperhumid (>1600).

Information sources

In order to obtain a list of the endemic taxa in the south of the Iberian Peninsula, we have used the listing of Rivas-Martínez et al. (1991) as a fundamental source. However, this listing has been updated using the volumes so far published of *Flora Iberica* (Castroviejo et al. 1986–2002), some other general works (Valdés et al. 1987; Blanca et al. 2002) and a number of recently published monographies and articles in scientific journals.

Taxa have been classified according to the following life form categories (Raunkiaer 1934): phanerophytes, nanophanerophytes, chamaephytes, hemi-cryptophytes, geophytes, therophytes, helophytes and hydrophytes. This classification is the result of an analysis of the already mentioned sources and our own field research.

Dispersal modes were determined with the aid of the records already published (Ridley 1930; Van der Pijl 1982; Murray 1986) or inferred from fruit morphology and our field observation. A total of nine categories appear, which depict the different dispersal modes observed: endozoochory, exozoochory, myrmecochory, anemochory because of small size, anemochory by means of pappi, anemochory due to wings, autochory, hydrochory and semachory/barochory (i.e., without clear morphological adaptations for seed dispersal).

There is no available information on the exact altitudinal distribution of many endemic taxa, nor on the rainfall rates in all the locations where they occur. However, with the help of published data and our own field experience, we have

been able to characterise each one of the endemic taxa by means of the thermotype and ombrotype where it occurs; it is not unusual to find populations of the same taxon in different categories.

Data analysis

A total of six species which could not be clearly ascribed have been excluded from this analysis. The relationships between the different characteristics have been studied by means of a correspondence analysis. Chi-square values have been used as similitude or association rates (Hair et al. 1999). Except when indicated, it has been assumed that p values below 5% reveal a statistically significant association. All the analyses have been carried out with the software utilities of STATISTICA 6.0 (StatSoft Inc. 2001).

Results and discussion

Altitudinal distribution

The total number of vascular endemic plants (species or subspecies) in the south of the Iberian Peninsula is 516, that is, ca. 13% of the whole flora. This percentage is quite similar to that of other surrounding areas and even lower than that of the Iberian Peninsula (Davis et al. 1994; Médail and Quézel 1997). However, the total number of exclusive endemisms is in fact relatively high in comparison with nearby areas (Melendo et al. 2003), since the south of the Iberian Peninsula has a high species richness. Another feature even more distinguishable is the endemism density, higher than that of other countries of the Mediterranean Basin (Figure 2). Besides, the endemism density in the highest parts of mountains is even higher than that of the Mediterranean and Macaronesian islands (Figure 2).

The largest number of endemic plants occurs in low and medium altitude mountainous areas (Figure 3). Particularly, in the low altitude mountainous areas or mesomediterranean belt, 235 endemic plants occur, for example, *Arenaria delaguardiae* G. López and Nieto Feliner, *Echinopartum algibicum* Talavera and Aparicio, *Eryngium grossii* Font Quer, *Iberis fontqueri* Pau, *Ononis varelae* Devesa, *Saxifraga reuteriana* Boiss., *Teline tribracteolata* (Webb) Talavera and P.E. Gibbs, and so forth. In the medium altitude mountainous areas or supramediterranean belt, there are 202 endemic taxa, such as *Alyssum gadorense* P. Küpfer, *Centaurea pulvinata* (Blanca) Blanca, *Herniaria baetica* Boiss. and Reuter in Boiss., *Hieracium texedense* Pau, *Laserpitium longiradium* Boiss., *Lithodora nitida* (Ern) R. Fernades and *Moehringia fontqueri* Pau.

In coastal areas, great depressions and valleys of the thermomediterranean belt, 156 endemic plants can be found, such as *Adenocarpus gibbisanus* Castrov. and Talavera, *Limonium malacitanum* Díez Garretas, *Linaria tursica* Valdés and Cabezudo, *Rosmarinus tomentosus* Huber-Morath and Maire, *Silene tomentosa* Otth in

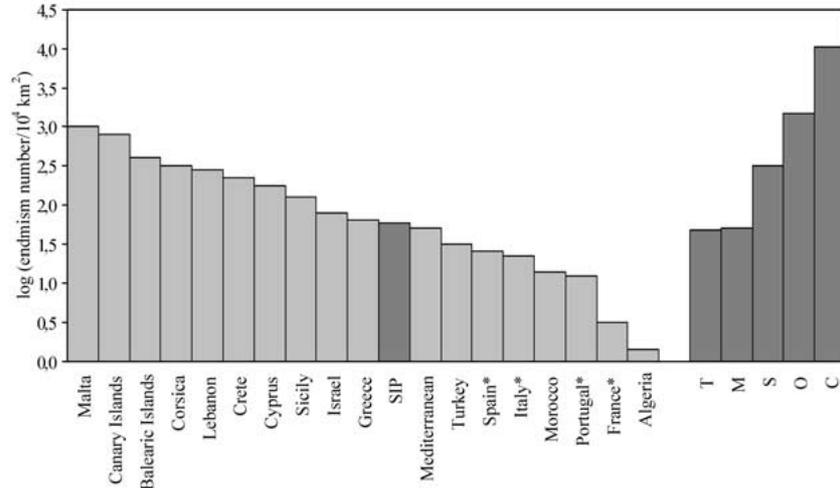


Figure 2. Endemism density of the south of the Iberian Peninsula (SIP) as a whole and by altitudinal belts in comparison with different countries and archipelagos of nearby areas. Data have been taken from Davis et al. (1994), Médail and Quézel (1997) and this study. The continental part of the respective countries is indicated by an *. T = thermomediterranean, M = mesomediterranean, S = supramediterranean, O = oromediterranean, C = cryoromediterranean.

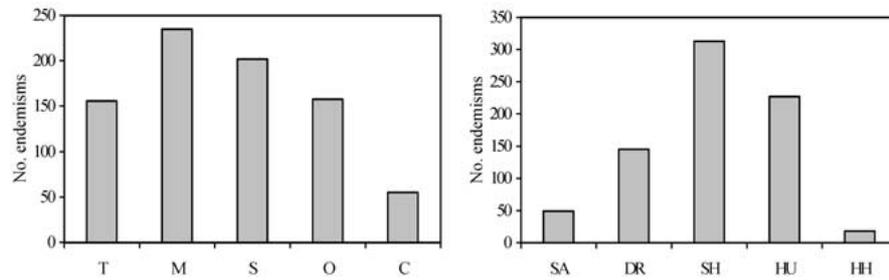


Figure 3. Number of endemic plants per thermotype (T = thermomediterranean, M = mesomediterranean, S = supramediterranean, O = oromediterranean, C = cryoromediterranean) and ombrotype (SA = semiarid, DR = dry, SH = subhumid, HU = humid, HH = hyperhumid).

DC., *Ulex canescens* Lange, and so forth. Almost the same number, 158, of endemic plants inhabit high mountain areas or the oromediterranean belt: *Astragalus tremolsianus* Pau, *Conoropus navasii* Pau, *Crepis granatensis* (Willk.) Blanca and Cueto, *Geranium cazorlense* Heywood, *Jurinea fontqueri* Cuatrec., *Senecio elodes* Boiss. ex DC., and so forth. The number of endemic taxa is dramatically lower, 55, in the cryoromediterranean belt, that is, the belt encompassing the highest peaks of Sierra Nevada. It is here that endemic species such as *Arenaria nevadensis* Boiss. and Reuter in Boiss., *Artemisia granatensis* Boiss., *Linaria glacialis* Boiss. or *Viola crassiuscula* Bory occur.

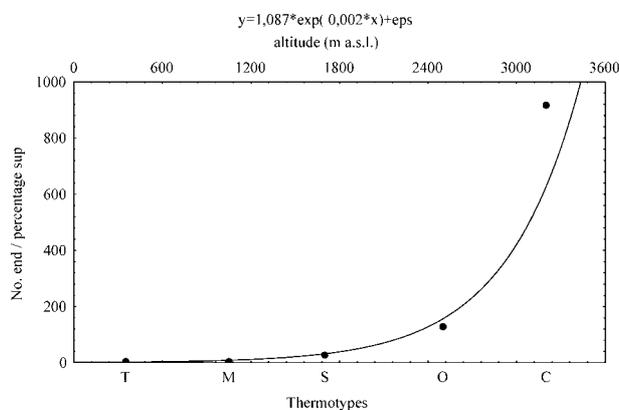


Figure 4. Floristic originality (rate of endemic taxa per area unit) in the south of the Iberian Peninsula related to the altitudinal gradient. T = thermomediterranean, M = mesomediterranean, S = supramediterranean, O = oromediterranean, C = cryoromediterranean.

However, if we bear in mind the extension of each of these altitudinal belts (Table 1), it is clear that floristic originality (number of endemic taxa per area unit) increases exponentially with altitude (Figure 4). According to Lobo et al. (2001), the environmental variable which most accurately accounts for the species richness in the Iberian Peninsula is altitudinal range. In general, species richness (number of taxa per area unit) decreases as altitude increases (Kitayama 1992; Stevens 1992; Vásquez and Givnish 1998; Odland and Birks 1999, etc.). A number of surveys, however, have shown that species richness, either of the whole flora (Rahbek 1995) or of particular taxonomical groups (Hemp 2002), reaches its highest values at medium altitudes. This can be explained by the fact that many species can adapt more easily to moderate environments but not to extremely adverse ones (Grace 1999; Van der Meulen et al. 2001). The endemic flora under study complies with neither of these patterns. The exponential growth of floristic originality as altitude increases reveals the fundamental role of geographical and ecological isolation in the process both of speciation and endemism. Consequently, in the area under study, and from a floristic point of view, full priority must be given, as far as preservation is concerned, to the high mountain areas of the Betic ranges.

The largest numbers of endemic taxa occur in areas of moderate rainfall (*Arenaria alfacariensis* Pamp., *Carex camposii* Boiss. and Reuter, *Erodium cazorlanum* Heywood, *Helianthemum pannosum* Boiss., *Verbascum nevadense* Boiss., etc.), and the number decreases towards the extremes of the rainfall gradient (Figure 3). According to Rey Benayas and Scheiner (2002), a negative correlation between local species richness and total rainfall reveals the limitations of many species in adapting to cold and flooding.

Unlike thermotypes, so far the extension of each ombrotype has not been estimated due to a lack of available information. Nevertheless, the dry ombrotype presents the widest extension, while, in mountain areas, subhumid and humid

ombrotypes tend to predominate. Thus, the abundance of endemic plants in these two rainfall rate intervals has much to do with the orophilous character of the endemic flora. The hyperhumid ombrotype extends around the Sierra de Grazalema, where there are few endemic plants (*Holcus grandiflorus* Boiss. and Reuter, *Linaria platycalyx* Boiss., *Saxifraga gemmulosa* Boiss., etc.). The case of semiarid areas, mostly located in the southeastern extreme of the territory, is more remarkable. Despite being a relatively small area, the number of endemic taxa here is comparatively high (Figure 3), with endemics such as *Antirrhinum charidemi* Lange, *Coris hispanica* Lange, *Euzomodendron bourgeanum* Cosson, *Limonium tabernense* Erben, *Linaria nigricans* Lange in Willk. and Lange, *Narcissus tortifolius* Fernández Casas and *Teucrium turredanum* Losa and Rivas Goday. The ecological isolation seems to play a significant role in this case, since the area is surrounded by the sea and high mountain ranges with higher rainfall rates.

Life forms

Figure 5A shows the life forms spectrum in the endemic flora as a whole. This spectrum is different from the spectra seen among local floras in both the south of the Iberian Peninsula (see, e.g., Cueto et al. 1991; Melendo and Cano 1998) and other areas of the Mediterranean Basin (see, e.g., Orshan 1986). The main differences are the very high percentage of chamaephytes and the low proportion of therophytes in the endemic flora. Contrary to phanerophytes, hemicryptophytes are also comparatively abundant in the endemic flora. Geophytes show similar percentages in both cases, but hydrophytes and helophytes have almost no endemic representation.

Most of the endemic species in the south of the Iberian Peninsula are chamaephytes (*Arenaria tomentosa* Willk., *Convolvulus boissieri* Steudel, *Cytisus galianoi* Talavera and P.E. Gibbs, *Hippocrepis eriocarpa* (Boiss.) Boiss., *Salvia candelabrum* Boiss., *Teucrium reverchonii* Willk., etc.) or hemicryptophytes (*Aquilegia nevadensis* Boiss. and Reuter in Reuter, *Cirsium gaditanum* Talavera and Valdés, *Echium albicans* Lag. and Rodr., *Erysimun rondae* Polatschek, *Gentiana sierrae* Briq., *Pinguicula vallisneriifolia* Webb, etc.). The rate of hemicryptophytes (31.37%) in the endemic flora is, generally speaking, high for the south of the Iberian Peninsula, but similar to the rates recorded among floras of some mountain areas (Cueto et al. 1991) and floras in temperate climates (see, e.g., Preston and Hill 1997). The rate of chamaephytes (46.08%) is considerably higher than the records observed among local or regional floras of the Mediterranean Basin (Quézel 1995).

Therophytes (*Arenaria retusa* Boiss., *Erodium recoderi* Auriault and Guittoneau, *Gaudinia hispanica* Stace and Tutin, *Omphalodes commutata* G. López, *Silene stockeni* Chater, etc.) represent 11.96% of the endemic flora, a record certainly close to 15%, the value estimated by Cowling et al. (1996) for local floras of any region with a Mediterranean climate. By contrast, the floristic analyses carried out in a number of sites of the Mediterranean Basin have recorded considerably higher rates of therophytes, up to 50% (Braun-Blanquet 1964; Melendo and Cano 1998).

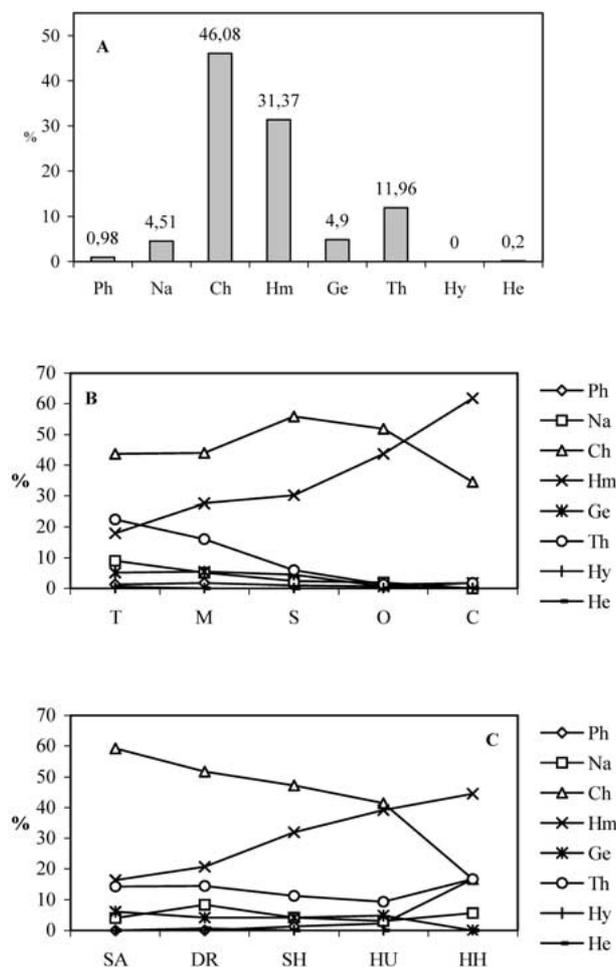


Figure 5. (A) Life form spectrum of the endemic taxa in the south of the Iberian Peninsula. (B) Life form distribution along an altitudinal gradient. (C) Life-form distribution along a rainfall gradient. Ph = phanerophytes, Na = nanophanerophytes, Ch = chamaephytes, Hm = hemicryptophytes, Ge = geophytes, Th = therophytes, Hy = hydrophytes, He = helophytes. T = thermomediterranean, M = mesomediterranean, S = supramediterranean, O = oromediterranean, C = cryromediterranean. SA = semiarid, DR = dry, SH = subhumid, HU = humid, HH = hyperhumid.

Figure 5B shows the distribution of the different life forms along the altitudinal gradient provided by thermotypes. Figure 5C shows the rate of each life form in relation to the rainfall gradient provided by ombrotypes. There is a statistically significant correlation between life form and both the altitudinal gradient and the rainfall gradient (Table 2). As far as distribution patterns are concerned, the three most representative life forms among endemic plants (chamaephytes,

Table 2. Results of the correspondence analysis applied to thermotypes and ombrotypes with regard to life forms (Ph = phanerophytes, Na = nanophanerophytes, Ch = chamaephytes, Hm = hemicryptophytes, Ge = geophytes, Th = therophytes, He = helophytes). Distance: chi-square.

	Ph	Na	Ch	Hm	Ge	Th	He
Thermotypes							
Thermomediterranean	0.04	8.40	-0.59	-9.50	0.53	19.00	3.37
Mesomediterranean	0.71	0.40	-0.70	-1.40	1.42	5.80	-0.29
Supramediterranean	-0.03	-1.40	2.78	-0.20	0.12	-4.60	-0.25
Oromediterranean	-0.33	-2.00	0.55	6.90	-4.42	-13.50	-0.20
Cryoromediterranean	-0.61	-2.30	-2.03	15.50	-0.64	-4.20	-0.07
$\chi^2 = 114.78; p < 0.0001.$							
Ombrotypes							
Semiarid	-0.78	-0.04	1.72	-3.49	0.34	0.31	-0.07
Dry	-2.31	4.09	0.88	-5.17	-0.02	1.06	3.38
Subhumid	-0.20	-0.17	0.05	0.05	-0.04	-0.04	-0.42
Humid	0.52	-1.20	-1.22	4.60	0.11	-1.05	-0.30
Hyperhumid	25.62	0.03	-3.43	1.00	-0.79	0.40	-0.02
$\chi^2 = 64.95; p < 0.0001.$							

hemicryptophytes and therophytes) behave quite differently in each of the gradients. The rest of the life forms seem to follow, with some exceptions, a more or less linear pattern with regard to the gradients of the analysis.

Chamaephytes are the most abundant species in all the thermotypes, with the exception of the cryoromediterranean, where hemicryptophytes are dominant. Chamaephytes exhibit their highest rate in medium altitude mountain areas or in the supramediterranean belt ($\chi^2 = 2.78$), whereas their rates tend to decrease towards the peaks of the cryoromediterranean belt ($\chi^2 = -2.03$). Their pattern is different as far as the rainfall gradient is concerned. In this respect, their rate decreases from semiarid to hyperhumid ($\chi^2 = -3.43$) areas.

The rate of hemicryptophytes increases along the altitudinal gradient, and they are positively correlated with the oromediterranean and cryoromediterranean belts ($\chi^2 = 6.90$ and $\chi^2 = 15.50$, respectively), and negatively with the thermomediterranean belt ($\chi^2 = -9.5$). A similar pattern can be seen along the rainfall gradient. Here, the correlation is negative with regard to the semiarid and dry ombrotypes ($\chi^2 = -3.49$ and $\chi^2 = -5.17$, respectively), and positive with regard to the humid ombrotype ($\chi^2 = 4.60$). Consequently, the abundance of hemicryptophytes is related to increasing rainfall rates and decreasing temperatures. These results are coincidental with records obtained in previous surveys of the Mediterranean Basin (Voliotis 1982; Danin and Orshan 1990).

When compared with hemicryptophytes, therophytes exhibit an inverse altitudinal distribution pattern: their rate tends to decrease as altitude increases. They present a clear positive correlation with the thermomediterranean belt ($\chi^2 = 19.00$) and a negative correlation with the oromediterranean belt ($\chi^2 = -13.50$). A number of surveys carried out in the Mediterranean Basin point to an optimum of

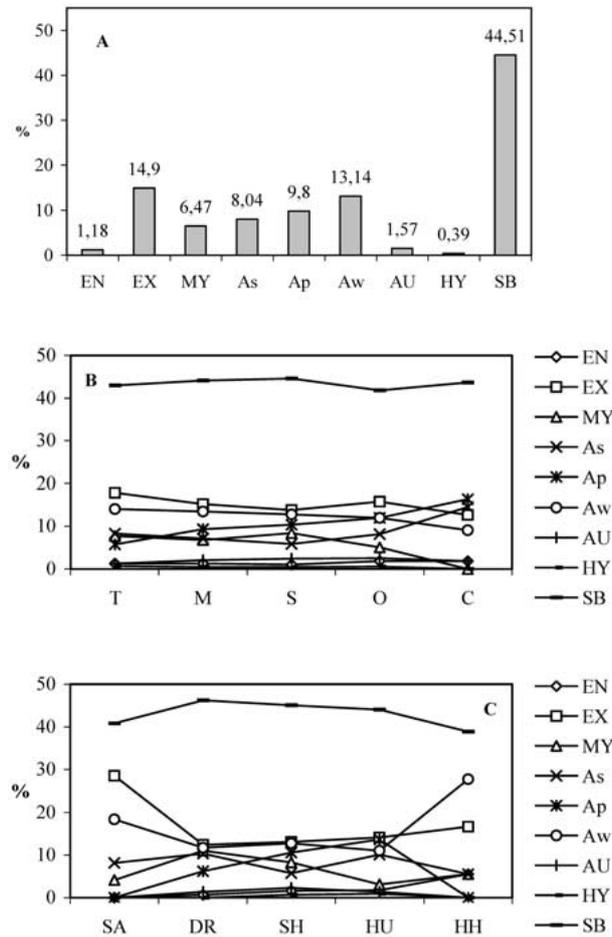


Figure 6. (A) Rates of endemic taxa in the south of the Iberian Peninsula per dispersal mode under consideration. (B) Distribution of dispersal modes among the endemic plants along an altitudinal gradient. (C) Distribution of dispersal modes along a rainfall gradient. EN = endozoochory, EX = exozoochory, MY = myrmecochory, As = anemochory due to small size, Ap = anemochory due to pappi, Aw = anemochory due to wings, AU = autochory, Hy = hydrochory, SB = semachory/barochory. T = thermomediterranean, M = mesomediterranean, S = supramediterranean, O = oromediterranean, C = cryromediterranean. SA = semiarid, DR = dry, SH = subhumid, HU = humid, HH = hyperhumid.

therophytes between 200 and 500 mm rainfall rates (Danin and Orshan 1990). This rainfall range lies within the semiarid and dry ombrotypes, but the data obtained in our survey for the endemic plants under study are different as far as both absolute and relative values are concerned. Absolute values of endemic therophytes in each ombrotype are: semiarid 7, dry 21, subhumid 35, humid 21, hyperhumid 3. Thus, the peak of abundance lies within the interval of 600–1000 mm rainfall.

Table 3. Results of the correspondence analysis applied to thermotypes and ombrotypes with regard to dispersal modes (EN = endozoochory, EX = exozoochory, MY = myrmecochory, As = anemochory due to small size, Ap = anemochory due to pappi, Aw = anemochory due to wings, AU = autochory, HY = hydrochory, SB = semachory/barochory). Distance: chi-square.

	EN	EX	MY	As	Ap	Aw	AU	HY	SB
Thermotypes									
Thermomediterranean	-0.01	0.68	0.30	0.06	-2.70	0.18	-0.50	0.07	-0.01
Mesomediterranean	-0.02	0.00	0.02	-0.11	-0.08	0.08	0.00	-0.03	0.02
Supramediterranean	-0.21	-0.30	1.05	-0.90	0.05	0.00	0.13	0.00	0.05
Oromediterranean	0.33	0.02	-0.54	0.04	0.71	-0.09	0.14	0.06	-0.11
Cryromediterranean	0.08	-0.25	-3.61	3.20	2.31	-0.62	-0.02	-0.27	0.00
									$\chi^2 = 19.94; p = 0.9522.$
Ombrotypes									
Semiarid	-1.92	7.93	-0.85	0.00	-6.08	0.25	-0.99	-0.30	-0.11
Dry	-0.79	-1.22	3.33	0.69	0.00	-1.30	0.16	-0.30	0.24
Subhumid	-0.05	-0.88	0.56	-0.63	3.27	-0.77	1.59	0.37	0.10
Humid	-0.01	-0.48	-1.73	0.58	9.44	-1.73	0.11	1.09	0.03
Hyperhumid	6.88	-0.01	-0.11	-0.74	-6.08	8.02	-0.99	-0.30	-0.40
									$\chi^2 = 73.44; p < 0.0001.$

Nevertheless, the weather of our study area is, in general, rainier than it is in Israel, where the previous survey took place, and in both cases a peak of abundance of therophytes was recorded within medium rainfall values. It seems wiser to consider relative values, since the extension of the different ombrotypes is very dissimilar. In this respect, there is no clear trend in the distribution of endemic therophytes along the rainfall gradient (Figure 5C).

Phanerophytes (*Abies pinsapo* Boiss., *Quercus alpestris* Boiss., etc.) do not exhibit any noteworthy correlation with regard to thermotypes, but they do with regard to the hyperhumid ombrotype ($\chi^2 = 25.62$). Nanophanerophytes (*Adenocarpus gibbsianus* Castrov. and Talavera, *Erica andevalensis* Cabezudo and Rivera, *Genista haenseleri* Boiss., *Ulex parviflorus* subsp. *rivasgodayanus* Cubas, etc.) are positively correlated with the thermomediterranean belt ($\chi^2 = 8.40$) and the dry ombrotype ($\chi^2 = 4.09$).

Dispersal modes

Figure 6A shows the species rate for each of the nine dispersal modes under consideration. The exozoochory rate (14.90%) exceeds the rate recorded in floras of temperate climates (Sorensen 1986; Willson et al. 1990). This is probably due to the fact that exozoochory plays a significant role in the survival of small populations in areas of a Mediterranean climate (Van der Pijl 1982; Shmida and Ellner 1983), as is the case in many endemic species. Endozoochory is frequent in floras of temperate climates (Buide et al. 1998), where it can be the dispersal mode of up

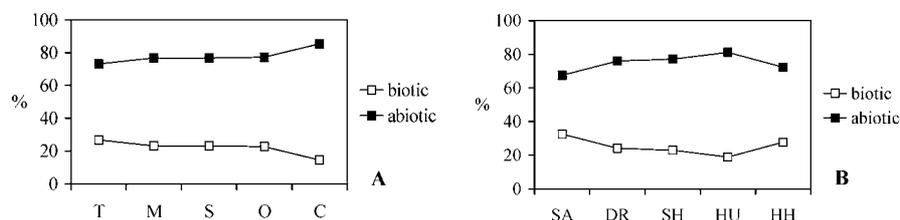


Figure 7. Distribution of biotic and abiotic dispersal modes among the endemic plants in the south of the Iberian Peninsula along altitude (A) and rainfall (B) gradients. T = thermomediterranean, M = mesomediterranean, S = supramediterranean, O = oromediterranean, C = cryromediterranean. SA = semiarid, DR = dry, SH = subhumid, HU = humid, HH = hyperhumid.

Table 4. Results of the correspondence analysis applied to thermotypes and ombrotypes with regard to biotic dispersion (endozoochory, exozoochory, myrmecochory) or abiotic dispersion (the rest). Distance: chi-square.

	Dispersal mode			Dispersal mode	
	Biotic	Abiotic		Biotic	Abiotic
Thermotypes			Ombrotypes		
Thermomediterranean	1.02	-0.29	Semiarid	2.13	-0.72
Mesomediterranean	0.06	-0.02	Dry	-0.05	0.02
Supramediterranean	0.06	-0.02	Subhumid	-0.21	0.07
Oromediterranean	0.02	0.00	Humid	-1.60	0.54
Cryromediterranean	-2.62	0.75	Hyperhumid	0.24	-0.08
	$\chi^2 = 4.84; p = 0.304.$			$\chi^2 = 5.67; p = 0.225.$	

to 50% of the species in some Mediterranean communities (Gutián and Sánchez 1992). Not surprisingly, it is, however, extremely infrequent among endemic floras (1.18%), since it implies the possibility of long-distance dispersal.

Up to 30.98% of the endemic plants present adaptations to anemochory. Certain extensions in the diaspores which act much in the same way as wings are particularly frequent (13.14%). Nevertheless, the most frequent category is semachory/barochory. A rate of 44.51% of the endemic species present no clear adaptations to promote dispersion. Although they sometimes benefit from other secondary mechanisms, their dispersal potential tends to be very limited. According to Cowling et al. (1996), the endemic plants of areas with a Mediterranean climate not only disperse badly, but also give rise to numerous sexually produced generations. Both facts account for their high rate of genetic recombination and fast speciation.

Figure 6 (B and C) shows the rates of the dispersal modes in relation to, respectively, the altitude and the rainfall gradients. There is no statistically significant correlation between the dispersal mode and the altitudinal gradient, but there is a clear correlation between the dispersal mode and the rainfall gradient (Table 3).

All the dispersal modes behave in a more or less uniform way with regard to the altitudinal gradient, with the exception of the anemochory due to pappi, whose rate

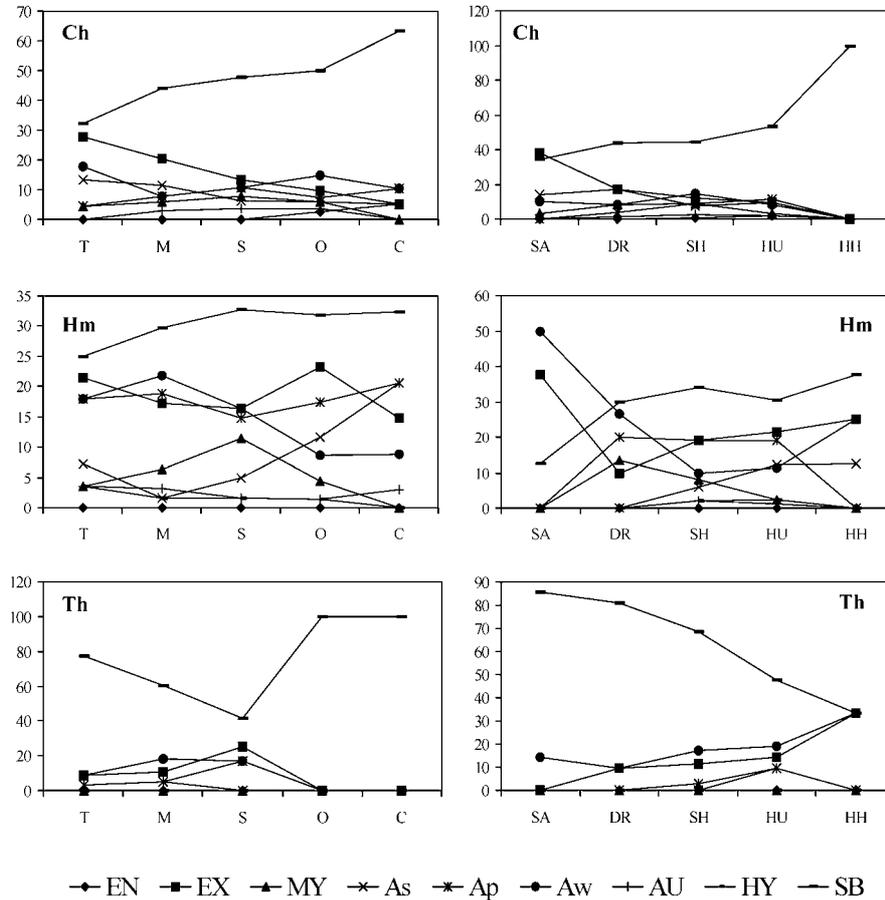


Figure 8. Distribution of dispersal modes along altitude and rainfall gradients in each of the three most abundant types of endemic plants in the south of the Iberian Peninsula: chamaephytes (Ch), hemi-cryptophytes (Hm) and therophytes (Th). T = thermomediterranean, M = mesomediterranean, S = supramediterranean, O = oromediterranean, C = cryomediterranean. SA = semiarid, DR = dry, SH = subhumid, HU = humid, HH = hyperhumid.

tends to increase with altitude (Figure 6B). Since pappi in diaspores can be an efficient long-distance dispersal mechanism, not surprisingly, it is frequent among endemic plants of isolated populations adapted to high altitudes, but relatively rare among endemic plants capable of inhabiting lower altitudes. On the other hand, as far as altitude is concerned, myrmecochory and wing anemochory show an inverse pattern. If we arrange all the dispersal modes into these two exclusive categories, biotic dispersion (endozoochory, exozoochory, myrmecochory) and abiotic dispersion (the rest), it will be clearly seen that, as altitude increases, biotic dispersion decreases whereas abiotic dispersion increases (Figure 7). Nevertheless, the correlation is not statistically significant (Table 4).

Table 5. Results of the correspondence analysis applied to thermotypes and ombrotypes with regard to dispersal modes (EN = endozoochory, EX = exozoochory, MY = myrmecochory, As = anemochory due to small size, Ap = anemochory due to pappi, Aw = anemochory due to wings, AU = autochory, HY = hydrochory, SB = semachory/barochory) in each of the three most abundant groups of endemic plants: chamaephytes (Ch), hemicryptophytes (Hm) and therophytes (Th). Distance: chi-square.

		EN	EX	MY	As	Ap	Aw	AU	HY	SB
Thermotypes										
Thermomediterranean	Ch	-0.53	5.29	-0.27	1.51	-1.11	1.87	-1.76		-2.53
	Hm		0.11	-0.25	-0.04	0.00	0.17	0.18	0.72	-0.31
	Th		-0.01		-0.89	0.94	0.00			0.02
Mesomediterranean	Ch	-0.81	0.82	-0.01	0.88	-0.02	-1.56	0.04		-0.03
	Hm		-0.08	0.02	-3.44	0.05	2.13	0.17	0.00	-0.03
	Th		0.33		0.02	8.14	10.75			-3.10
Supramediterranean	Ch	0.88	-0.74	0.76	-0.88	0.94	-0.16	0.39		0.15
	Hm		-0.18	3.28	-0.80	-0.28	0.01	-0.13	0.00	0.07
	Th		29.68		27.66	-1.62	7.21			-15.42
Oromediterranean	Ch	2.91	-2.30	0.00	-0.68	-0.05	0.51	0.36		0.39
	Hm		0.73	-0.27	0.97	0.00	-1.76	-0.24	-0.01	0.02
	Th		-8.82		-4.96	-1.62	-8.73			7.68
Cryoromediterranean	Ch	4.92	-1.47	-1.13	-0.27	0.15	-0.03	-0.49		1.33
	Hm		-0.30	-1.99	6.36	0.18	-0.83	0.05	-0.53	0.03
	Th		-8.82		-4.96	-1.62	-8.73			7.68
		Ch: $\chi^2 = 40.95$; $p = 0.05$.		Hm: $\chi^2 = 26.79$; $p = 0.53$.					Th: $\chi^2 = 169.42$; $p < 0.0001$.	
Ombrotypes										
Semiarid	Ch	-0.56	32.97	-0.33	1.80	-4.90	0.48	-1.23		-7.81
	Hm		9.88	-4.72	-6.17	-11.62	26.28	-0.62	-0.85	-9.28
	Th		-13.72		-1.90	-2.48	-1.03			7.99
Dry	Ch	-0.56	0.24	2.35	6.17	-0.16	-0.01	0.01		-2.29
	Hm		-7.00	15.74	-6.17	6.04	0.18	-0.62	-0.85	0.04
	Th		-1.28		-1.90	-2.48	-4.48			4.97

Table 5. (Continued)

	EN	EX	MY	As	Ap	Aw	AU	HY	SB
Subhumid	Ch	0.02	-0.68	3.58	-0.50	3.08	5.10	1.75	-2.06
	Hm		-0.57	2.29	-0.01	4.69	-8.65	3.03	0.91
Humid	Th		-0.38		-1.90	0.06	-0.13		1.56
	Ch	4.37	-2.21	-0.48	0.00	9.46	0.00	0.65	-0.08
	Hm		-0.07	-1.29	6.20	4.81	-7.24	0.39	0.08
	Th		0.02		30.46	20.04	0.01		-3.86
Hyperhumid	Ch	-0.56	-15.40	-4.68	-9.63	-4.90	-8.34	-1.23	36.23
	Hm		0.26	-4.72	6.49	-11.62	0.01	-0.62	2.58
	Th		28.06		-1.90	-2.48	11.52		-14.14
	Ch:	$\chi^2 = 176.87; p < 0.0001.$							
				Hm: $\chi^2 = 177.30; p < 0.0001.$					
								Th: $\chi^2 = 157.63; p < 0.0001.$	

Although the correspondence analysis reveals a significant correlation between the dispersal mode and the rainfall gradient (Table 3), no clear trend can be seen in Figure 6C. The clearest positive correlations are the following: endozoochory and wing anemochory with the hyperhumid ombrotype ($\chi^2 = 6.88$, $\chi^2 = 8.02$); exozoochory with the semiarid ombrotype ($\chi^2 = 7.93$); myrmecochory with the dry ombrotype ($\chi^2 = 3.33$); and anemochory due to pappi with the humid ombrotype ($\chi^2 = 9.44$). Trends are more evident if, instead of considering the endemic flora as a whole, the analysis is applied separately to each of the most abundant groups of biological forms (Figure 8, Table 5). For example, semachory/barochory exhibits different patterns among therophytes on the one hand, and chamaephytes and hemicryptophytes on the other. As already mentioned, the occurrence of therophytes is positively correlated with the thermomediterranean belt. In these low areas of valleys and depressions, the geographical isolation does not play an important role, whereas a limited potential for dispersion, by contrast, contributes significantly to the maintenance of stenochory.

Conclusions

In the south of the Iberian Peninsula, the distribution patterns for the endemic vascular flora along the altitude and rainfall gradients are different to those for the whole flora. Despite the fact that the highest number of endemics is located at medium altitudes (between 600 and 1400 m a.s.l.) and at intermediate ranges of rainfall (from 600 to 1000 mm), the major floristic originality (number of endemics per area unit) is reached in high mountain areas.

The biological spectrum of this endemic flora does not follow the usual models observed either in the local floras of the south of the Iberian Peninsula or in other regions of the Mediterranean Basin. This biological spectrum is as related to the altitude gradient as it is to the humidity one, but it cannot be exclusively explained by the distribution patterns; other factors such as taxonomic composition or dispersal mode must be taken into account.

The geographical and ecological isolation plays a much more important role in the speciation and endemism of the south of the Iberian Peninsula flora than the limitations of the dispersal strategies, despite the fact that almost half of these endemics do not present evident dispersal adaptations. However, in the group of therophytes, whose occurrence is positively related to areas of minor altitude, this difficulty of dispersal does play a significant role in the maintenance of stenochory.

Major efforts for the conservation of the south of the Iberian Peninsula flora must be centred in the high mountain areas. Most of these areas have been declared as a Natural Park or National Park (Sierra Nevada), but there are still interesting areas without legal protection, such as Sierra de Gádor. Other areas of great interest for the conservation of this endemic flora are the semiarid depressions of the southeast of the Iberian Peninsula. Anyhow, conservation policies for each area must be established according to the peculiar features, life forms and dispersal modes of its endemic flora.

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