

Patterns and traits of the endemic plants of Greece

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Greece is characterized by high plant diversity (5800 species) and endemism (15.6%). This study attempts a first overall assessment of the taxonomy, distribution, traits and conservation status of the Greek endemic plants. The endemic species belong to 56 families and 242 genera. Most of the endemic plants have a narrow geographical and altitudinal distribution range. The southern floristic regions are richer in endemic species. The species area relationships for endemics (EARs) for island and continental floristic regions explain over 50% of the variation in number of species and are characterized by steep curves. Analysis of the distributional pattern of the endemics by similarity coefficients offers useful insights into the palaeogeography and biogeography of Greece. The endemic species occur at all altitudes, but the altitudinal distribution shows a predominance of local endemics at 0–600 m in the island regions and in higher zones in the continental regions. The life form spectra show a predominance of hemicryptophytes and chamaephytes. This trait seems indicative of their habitat and adaptive strategy and may be related to speciation processes. The overview of the conservation status of the Greek endemics indicates that over 40% of the taxa are threatened or near threatened. © 2010 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2010, **162**, 130–422.

ADDITIONAL KEYWORDS: altitudinal distribution – conservation – distribution – endemism – floristic analysis – life form – phytogeography – plant diversity.

INTRODUCTION

Greece is phytogeographically a borderline and a crossroads, an eastern Mediterranean and a Balkan country, the south-easternmost edge of Europe in immediate contact with South-West Asia and close contact with North Africa. Its high mountains and islands have acted through geological history as stepping stones and refuges for taxa of the surrounding floristic regions and as isolation centres. Mediterranean-type ecosystems cover more than 90% of Greece, the vegetation belts ranging from xerothermo- to cryo-Mediterranean (Hobbs, Richardson & Davis, 1995). In broad terms, the complicated geological history, dissected topography and varied bioclimate are the main reasons for the floristic diversity and increased endemism in Greece (Iatrou, 1986; Thompson, 2005).

Despite active botanical exploration and study, the general reference literature for the flora of Greece is segmental and a great part of it not updated. The early 20th century floras, Conspectus Florae Graecae (Halácsy 1901-1904, 1908, 1912), Prodromus Florae Peninsulae Balcanicae (Hayek 1924–1933) and Flora Aegaea (Rechinger, 1943a) include only parts of Greece. The more recent Med-Checklist (Greuter, Burdet & Long, 1984, 1986, 1989) covers a number of families and the Mountain Flora of Greece (Strid, 1986; Strid & Tan, 1991) covers the mountain-alpine region. The flora of the Cretan area is exceptionally well investigated (Rechinger, 1943b; Greuter, 1973; Greuter, Matthäs & Risse, 1984a, 1984b, 1985; Bergmeier & Matthäs, 1995) and there are recent floras and checklists (Turland, Chilton & Press, 1993; Jahn & Schönfelder, 1995; Chilton & Turland, 1997). Flora Europaea (Tutin et al., 1968–1980, 1993) excluded the East Aegean islands which were included in the Flora of Turkey and the East Aegean Islands (Davis, 1965-1986). Otherwise, the data are scattered across 13 276 published papers, monographs and theses (Strid, 2006) and in unpublished herbarium material. Recent floristic and taxonomic activity in Greece has resulted in significant additions, exclusions and changes in taxonomic status (Strid & Papanikolaou, 1985; Tan & Iatrou, 2001). The Flora Hellenica

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project will eventually bridge the gaps: the first two volumes have been published (Strid & Tan, 1997, 2002), but the completion of the project will take several more years.

In the meantime, conservationists lack an overall assessment of Greek endemic species. The most recent complete catalogue of Greek endemic plants listed 752 species (IUCN, 1982), a number later corrected to 742 (WWF & IUCN, 1994) which has since been quoted in the literature (Phitos *et al.*, 1995; Strid & Tan, 1997). Apart from that, there is a recent endemic flora (Tan & Iatrou, 2001) of the Peloponnese (Peloponnisos) and a report of the disparately greater figure of a total of 1275 endemic taxa in Greece (Iatrou, 1996).

Phytogeography and endemism have been studied in the Aegean (Rechinger, 1949; Rechinger & Rechinger-Moser, 1951; Snogerup, 1967a; Runemark, 1969, 1970, 1971a, b, Strid, 1970, 1972, 1996; Greuter, 1972, 1975; Cardona & Contandriopoulos, 1978; Carlström, 1987; Christodoulakis, 1996; Panitsa et al., 2006; Panitsa, Tzanoudakis & Sfenthourakis, 2008), Peloponnisos (Iatrou, 1986) and Evvoia (Trigas, 2003). The origin and distribution patterns of the Greek flora and the endemics have been connected to palaeogeographical patterns (e.g. Turrill, 1929; Rechinger, 1965). The palaeogeographical evolution of the area of Greece, the Hellenic orogen, a composite segment of the Alpine orogen, is relatively recent and complex. The Hellenic arc lies in an active geological region created by the late Mesozoic and Cenozoic collision of the European and African plates and is the result of processes including south(west)ward rollback of subducting African lithosphere and associated backarc extension, gravitational collapse and westward extrusion of Anatolia (e.g. Doutsos et al., 1993; van Hinsbergen, 2004; Mountrakis, 2006). The mountain range of the Hellenides with a continental mass the Aegais connected the Balkans with Asia Minor until the Miocene (13 Mya) when the fragmentation of Aegais started (Creutzburg, 1966; Dermitzakis, 1990). Crete (Kriti) in the South Aegean Arc was first separated 10 Mya (Creutzburg, 1966; Sissingh, 1976; Dermitzakis, 1990) and 9 Mya the mid-Aegean Trench separated the eastern Aegean islands and Asia Minor from the Cyclades and mainland Greece (Dermitzakis & Papanikolaou, 1981). During the Messinian desiccation of the Mediterranean, connection among certain areas was re-established (Hsü et al., 1978; Andersen et al., 2001), although deep canyons with unfavourable climatic conditions must have acted as dispersal barriers. By early Pliocene the South Aegean Arc split once more and Kriti was permanently isolated (Meulenkamp, 1985; Beerli, Hotz & Uzzell, 1996), while the North Anatolian fault propagated into the north Aegean region in late Pliocene time (Dinter, 1998). The onset of a Mediterranean-type climate is placed in the midPliocene (Suc, 1984; Pons & Quézel, 1985; Bertoldi, Rio & Thunell, 1989; Suc *et al.*, 1994). During the Pliocene and Pleistocene, certain areas were submerged and then re-emerged and connections among islands and mainland landmasses were established or broken in a complex sequence of events affecting the organisms inhabiting the area (Dermitzakis & Papanikolaou, 1981; Dermitzakis, 1990; Schúle, 1993; Sfenthourakis, 1996; Hausdorf & Hennig, 2005; Kasapidis *et al.*, 2005; Poulakakis *et al.*, 2005; Simaiakis & Mylonas, 2006; Comes, Tribsch & Bittkau, 2008).

The extant Greek flora is typically Mediterranean with 'Palaeo-Mediterranean' tropical and subtropical taxa which evolved during the pre-Pliocene and Pliocene (remnants of a flora that became extinct during the glaciations) and 'Neo-Mediterranean' nontropical taxa which appeared after the establishment of Mediterranean type climate (for a review see Blondel & Aronson, 1995). The flora has been influenced by east-to-west migration during the Miocene and by a north-to-south migration in consecutive waves (Iatrou, 1986). A part of the endemic flora represents species the ancestors of which had a broader distribution during the Tertiary (Turrill, 1929). The South Aegean element of the flora correlated to the South Aegean Arc reflects the situation during the Miocene and the Cardaegean element (the Cretan area and the South and Central Cyclades) reflects the situation during the Pleistocene (Greuter, 1971, 1975). In the Cyclades there has been active differentiation of endemics inside numerous islands (Cardona & Contandriopoulos, 1978). The endemic flora of Kriti has a relict character, but with a nonnegligible neoendemic element (Greuter, 1972; Cardona & Contandriopoulos, 1978). Recent molecular studies (Bittkau & Comes, 2005; Edh, Widén & Ceplitis, 2007) support the theory that plant diversification and speciation in the Aegean region is driven mainly by random (genetic drift) rather than adaptive differentiation among isolated populations (Runemark, 1969; Strid, 1970; Snogerup, Gustafsson & von Bothmer, 1990; Thompson, 2005). The flora of Peloponnisos and the mountain flora are characterized by a large proportion of neoendemics, indicating active speciation processes (Strid & Papanikolaou, 1985; Iatrou, 1986) and, on the whole, it is assumed that there are more neo-endemics than palaeondemics in the Greek flora (Tan & Iatrou, 2001; Thompson, 2005). According to the above sources, it seems that two processes, the evolution of habitat specialists (e.g. serpentine endemics) and of vicariant taxa (e.g. islet specialists) have been important in endemic species formation.

The aim of this paper is to present, for the first time, quantitative data on the taxonomy, geographical and altitudinal distribution, ecology (life form) and conservation status of all the Greek endemic plants

and investigate their traits and possible relationships. The study of the above aspects, besides revealing general patterns of endemism in Greece, can also be used for conservation purposes. The pattern of distribution of species in genera and families is useful in making decisions targeting conservation effort (Fenner, Lee & Bastow Wilson, 1997). The same is true for geographical and altitudinal distribution (e.g. Gómez Campo & Malato Beliz, 1985; Cowling & Samways, 1995a; McDonald & Cowling, 1995; Médail & Verlaque, 1997; Roos et al., 2004) and species-area relations can be used to predict extinction (Reid, 1992; Whittaker & Fernández-Palacios, 2007). Life form, a functional or adaptive plant attribute (Box, 1987; Médail, Roche & Tatoni, 1998), seems to have a predictive value for conservation in the Mediterranean (Verlague, Médail & Aboucava, 2001) and for the impacts of global climate change (Broennimann et al., 2006; Thuiller et al., 2006). Inherently, this work is intended as an incentive for further research into and cooperation on the knowledge, understanding and hence the conservation of the endemic plants.

MATERIAL AND METHODS

The data set used in this study was derived from the database Chloris (Georghiou & Delipetrou, 1990–2009). Chloris is a relational MS Access database with coded data on the taxonomy, distribution, biology, ecology, conservation and protection status of the endemic, subendemic, rare, threatened and protected plants of Greece. It is regularly updated and currently contains data on 3222 taxa of Pteridophyta and Spermatophyta based on all the relevant floras, another 1130 published literature sources and 180 not published (including Internet) valid sources.

The term 'Greek endemic' denotes vascular plant taxa that occur only within the political borders of Greece. This is quite straightforward for the islands, but there are at least eight stenoendemic mountain taxa occurring just on both sides of the borders with Balkan countries. Such taxa were not included in data analysis. However, it must be noted that the inclusion of these taxa in the data sets used for the calculation of indices or in statistical analysis had no significant effect on the results (data not shown).

Distribution data are coded using the 13 floristic regions of Greece (Fig. 1) in the Flora Hellenica project (Strid & Tan, 1997) in which the division of the Aegean was mainly based on Rechinger (1943a, 1949), confirmed by floristic data from Strid (1996). The continental regions are: Peloponnisos (Pe), Sterea Ellada (StE), South Pindos mountain range (SPi), North Pindos mountain range (NPi), East Central Greece (EC), North Central Greece (NC), North-East Greece (NE). The island regions are: West Aegean islands, including the large island of Evvoia (WAe); Ionian Islands (IoI), North Aegean islands (NAe), the island complex of the Cyclades (Kik), Cretan area including the large island of Kriti and its surrounding islets and the islands of Kasos and Karpathos (KK), East Aegean islands (EAe). Life form data are coded according to Raunkiaer (Ellenberg & Müller-Dombois, 1966; Pignatti, 1982).

The vegetation zones used in the altitudinal distribution of plants correspond to the altitude range classes in Table 1. This is a rough correspondence, as the exact range of each zone in Greece varies, not only depending on latitude but also locally (e.g. southern and northern slopes).

Species-area relationships for all species (SARs) and for endemic (i.e. endemic to one floristic region) species (EARs) within the Greek floristic regions were investigated assuming the 'power equation' with logarithmic transformation:

$\log S = c + z \log A$ (S = species number; A = area; c, z = constants)

Hierarchical cluster analysis was carried out using the STATISTICA software and was based on the presence/absence of species or taxa in each floristic region. A preliminary analysis was made with the use of three linkage methods (single, complete and unweighted pair-group average), each applied using four measures of similarity: Dice (Chekanowski or Sørensen, matches weigh double, joint absences excluded), Jaccard (equal weight to matches and nonmatches, joint absences excluded), Lance-Williams (Bray-Curtis, complementary to Dice) (eqn. 1) and the Preston index (eqn. 2), which is not greatly affected by large differences in the number of taxa (or the area) of the regions compared (Preston, 1962). Indices that include joint absences (e.g. Hamman) were deemed inappropriate because a large number of taxa occur in only one floristic region and are absent from all others and this would result in artefactual relationships between non-similar regions.

Lance–Williams index =
$$(b + c)/(2a + b + c)$$
 (1)

where a = number of taxa present in both of the pair of regions compared; b and c = taxa present on one region but absent from the other.

$$\left(F_{1}/F_{1+2}\right)^{n} + \left(F_{2}/F_{1+2}\right)^{n} = 1 \tag{2}$$

Preston index z = 1/n; F_1 and F_2 = number of species present in each of the pair of regions compared; F_{1+2} = total number of species present in the pair of regions compared. The equation was solved for each pair of regions by the MSExcel solution tool.

The available data on the conservation status of the Greek endemic plants (see references in the relevant

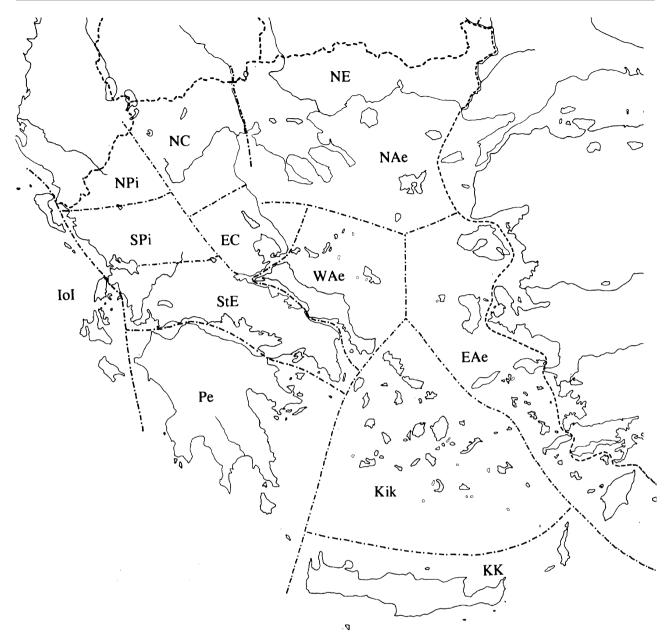


Figure 1. The floristic regions of Greece (Strid & Tan, 1997).

Zone	Altitude range (m)	Description
A	0–600	Thermo-Mediterranean: Eu-Mediterranean matorral and thermophilous conifer zone (coastal, hilly, submountainous)
В	600 - 1000	Meso-Mediterranean: Sub-Mediterranean shrub and forest (hilly, submountainous)
С	1000 - 1500	Supra-Mediterranean: Fagus and Abies forest zone (including sub-Mediterranean conifers)
D	1500 - 2000	Mountain Mediterranean: Boreal conifer (e.g. Picea) zone
Е	2000-3000	Oro-Mediterranean/Alpine. No forests

Table 1. Correspondence of vegetation zones to altitude range classes

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Region	Area km ²	Native species	sp/ <i>log</i> area	<i>log</i> sp/ <i>log</i> area	Endemic species	% Endemic	Source*
Greece	132 700	$5\ 855$	1143	0.74	913	15.6	1, 2, 3
Cyprus	9251	$1\ 612$	406	0.81	110	6.8	5, 4
Bulgaria	111 000	$3\ 600$	714	0.70	320	8.9	6
Italy (territory)	$301\ 049$	$5\ 300$	967	0.68	712	13.4	7
France (territory)	$551\ 700$	$4\ 650$	810	0.64	133	2.9	6
Peninsular Spain (+ Balearics)	$501\ 000$	$7\ 920$	1390	0.68	550	6.9	8
Canary Islands	$14\ 879$	$1\ 800$	431	0.78	550	30.6	8
UK	$244\ 754$	$1\ 800$	334	0.60	16	0.9	6, 9
Turkey	$779\ 500$	$8\ 650$	1468	0.67	$2\ 675$	30.9	10
Morocco	$710\ 850$	$3\ 675$	628	0.61	625	17.0	6
Southern Africa	$2\ 570\ 000$	$20\ 372$	3178	0.67	$16\ 298$	80.0	11
Madagascar	$587\ 000$	10 000	1734	0.69	8 000	80.0	6
Chile	$462\ 820$	$4\ 669$	824	0.65	$2\ 700$	57.8	6, 12
California (MTE)	$242\ 519$	$5\ 050$	938	0.69	$1\ 515$	30.0	13
Argentina	$2\ 770\ 000$	$9\ 370$	1454	0.62	1 100	11.7	6
Panama	$75\ 648$	9 900	2029	0.82	$1\ 222$	12.3	6
Venezuela	$1\ 148\ 154$	$21\ 070$	3477	0.71	8 000	38.0	6

Table 2. Species diversity and endemism in regions of the Mediterranean, Europe, Africa and South America

*Sources: 1, Strid & Tan, 1997; 2, Tan & Iatrou, 2001; 3, Chloris database; 4, database CyprusFlora; 5, Hadjikyriakou, 1997; 6, WWF & IUCN, 1994; 7, Pignatti, 1995; 8, Bueno *et al.*, 1995; 9, WWF & IUCN, 1988; 10, Davis, 1965–1986; 11, Cowling & Hilton-Taylor, 1994; 12, Fuentes *et al.*, 1995; 13, Keeley & Swift, 1995.

section of the results) include classification in: (1) the old, pre-1994 IUCN categories (Lucas & Synge, 1978); (2) the new IUCN categories, according to the 1994 version (Mace & Stuart, 1994); and (3) the new IUCN categories, according to the revised 2001 version (IUCN, 2001). The conservation status of the plants that have been classified only according to the pre-1994 IUCN categories [i.e. extinct (Ex), endangered (E), vulnerable (V), rare (R), not threatened (nt), indeterminate (I), inadequate data (?)] was not transferred to the new categories because there is no reliable correspondence, except from the old category inadequate data (?), which was transferred to the new category Data Deficient (DD) and from the old category not threatened (nt) which was transferred to the new category Least Concern (LC). The conservation status of the plants classified according to the 1994 version was transfered to the 2001 version on a case-by-case reassessment.

RESULTS

BIODIVERSITY AND ENDEMISM

Taking species richness in relation to area size as a measure of biodiversity, Greece, with an estimated 6437 native plant taxa or c.5800 species (Strid & Tan, 1997, 2002; Tan & Iatrou, 2001), ranges among the highest in European and Mediterranean or Mediterranean-type climate areas (Table 2).

Table 3. Greek endemic species and taxa

	Endemic sexual	Endemic apomictic	? Endemic	Doubtful taxa	Total
Species*	913	65	27	56	1061
Subspecies	345	1	28	37	411
Varieties	24		2	5	31
Taxa	1226	66	52	98	1442

*Fifty species with infraspecific subdivisions.

The vascular plant species recorded in the database Chloris as endemic to Greece number 1061 (1442 taxa) (Table 3). Even excluding apomictic species and species doubtfully endemic or of doubtful taxonomic status, this number becomes 913 species (1226 taxa). Species endemism reaches 15.6% of the total native flora which, taking into account the small area of the country, is quite high in comparison with other Mediterranean-type climate and European countries (Table 2). Using Bykov's index (*le* = endemism factual/ endemism normal) (Fig. 2) as a quantitative measure of endemism (Cowling & Samways, 1995b), Greece has 2.1 times the normal endemism for its area, which is lower than South Africa (le = 3.6) or the exceptionally high-ranking Canary Islands (le = 9.3), but comparable with Turkey and Cyprus (le approximately 2) and higher than Bulgaria, Italy, Peninsular

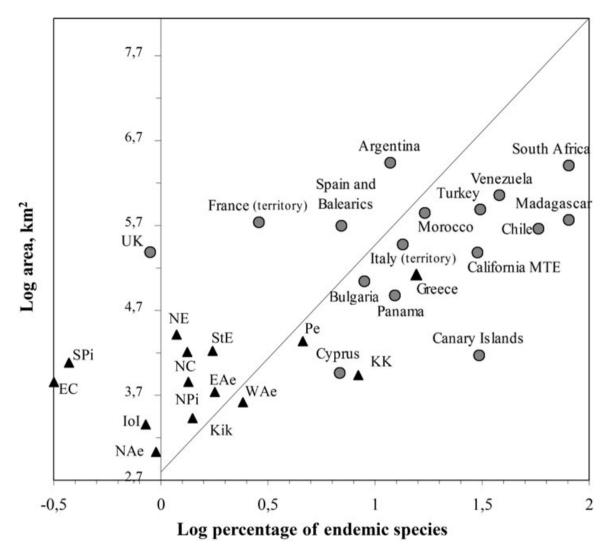


Figure 2. Bykov's nomogram. The diagonal line is defined by 100% endemism for the earth and by 1% endemism in 625 km² and depicts normal endemism (*En*). Points represent the factual endemism (*Ef*). Areas above the diagonal line have less than normal endemism and areas below the line have more. Data for Greece and the Greek floristic regions do not include doubtful or apomictic species.

Spain and the Balearics and Morocco (le = 0.7-1.2). Within the floristic regions of Greece, the Cretan area (le = 3.1) is indicated as the most important centre of endemism, a well-known fact commented upon by Greuter (1972), Rechinger (1949, 1965) and Strid, 1986. Peloponnisos and the West Aegean (le = 1.2) are the only other regions exceeding the expected endemism. The East Aegean islands and the Cyclades have close to normal levels of endemism (le = 0.8).

FLORISTIC ANALYSIS

The endemic species (apomictic and doubtful species included) belong to 53 families and 239 genera. There are no endemic families and there are six monotypic endemic genera: *Horstrissea* Greuter, P.Gerstberger & B.Egli, Jankaea Boiss., Peltaria Jacq., Petromarula Vent. ex R.Hedw., Phitosia Kamari & Greuter and Thamnosciadium Hartvig. The families richer in endemic species in absolute numbers (Fig. 3) are Asteraceae, Caryophyllaceae, Brassicaceae and Lamiaceae. Their degree of endemism (27, 30, 24 and 22%, respectively) is higher than that of the general flora (15.6%). However, the highest degree of endemism is seen in Campanulaceae (49%). At infraspecific level, the endemic taxa belong to 58 families and 281 genera.

The genera of the endemic species are presented in Figure 4. The total species/genus ratio in the endemics is 4.4, and 45% of the genera have only one endemic species. However, certain genera, notably *Centaurea* L., *Campanula* L., *Silene* L., *Allium* L.,

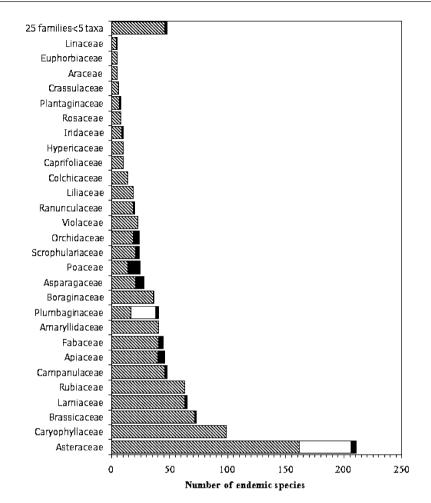


Figure 3. The families of the Greek endemic species: sexual species (striped bar), apomictic species (open bar) and doubtful species (black bar).

Verbascum L., Ophrys L., Viola L. and Stachys L., show a high degree of species richness and endemism (endemic/all species: 61/122, 42/77, 38/119, 39/79, 23/72, 40/90 and 17/52, respectively). [Species concepts and the number of species recognized in Ophrys vary considerably between authors. Here, a relatively narrow concept is used, but it should be noted that this may result in an over-representation of this genus in these analyses. For example, in the recent treatment of Pedersen & Faurholdt (2007), no Ophrys spp. are endemic to Greece, although some infraspecific taxa are.]

DISTRIBUTION IN FLORISTIC REGIONS

The majority of the endemic species are restricted to only one floristic region (Fig. 5) and none occurs in all 13 regions. The distribution across regions (Fig. 6) shows that southern and eastern Greece is richer in absolute numbers of endemics. Peloponnisos, the Cretan area and Sterea Ellada are the regions with the highest numbers of endemic species, in descending order, and the Cretan area has the highest number of local endemics (173 species, 235 taxa, excluding apomictic and doubtful taxa).

The species-area relationships for all species (SARs) and for endemic species (EARs) are shown in Figure 7. The SAR for the 13 floristic regions (species numbers according to Tan & Iatrou, 2001) was highly significant with a z-value (the regression coefficient) of 0.20 and explained a considerable amount of species number variation (76%). The analysis for continental and island regions separately resulted in a significant SAR with a steeper slope (z = 0.38) and a high \mathbb{R}^2 (0.87) for the continental regions and, in SAR significant only at 1% error level, with a shallower slope (z = 0.14) and lower \mathbb{R}^2 (0.54) for the island regions. The EAR for all the floristic regions was not significant and explained only a low percentage of species number variation. The EAR for the island regions was significant with a steep curve (z = 1.15) and 82% of the variation in the number of endemics was explained by the total size of the islands per region. The EAR for the continental regions

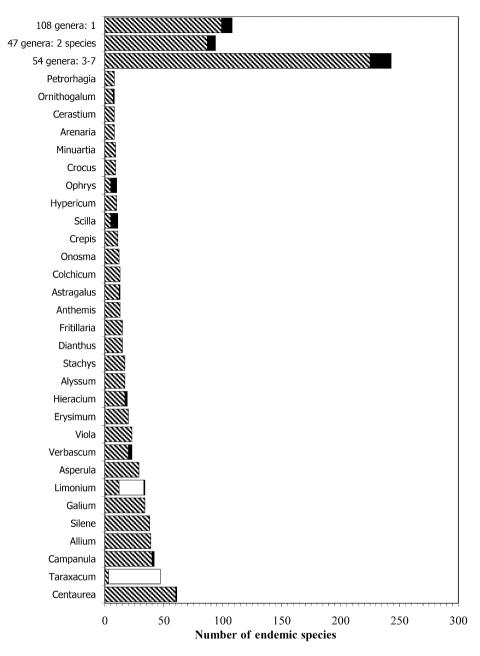


Figure 4. The genera of the Greek endemic species: sexual species (striped bar), apomictic species (open bar) and doubtful species (black bar).

resulted in an equally steep curve (z = 1.49), which explained 46% of the variation in the number of endemics but was significant only at 1% error level. The respective *c*-values (island c = -2.5, continental c = -4.7) indicate that continental regions with a lower initial slope have fewer endemics per unit area. All types of EARs gave similar results when the doubtful and apomictic species were excluded or for the endemic taxa, i.e. with subspecies and varieties included. The performance of the semi-log model was worse in all cases (data not shown). Analysis of the distributional pattern of the endemics and of the relations among floristic regions, based on their common endemic taxa, was made by hierarchical clustering (Fig. 8). The preliminary analysis resulted in two distinct classification patterns for each linkage method, which were essentially similar for the species and the taxa data sets, regardless of whether apomictic and doubtful taxa were included: one using the Lance–Williams dissimilarity coefficient, which was identical to the classification with Dice and Jaccard, and one using the Preston z dis-

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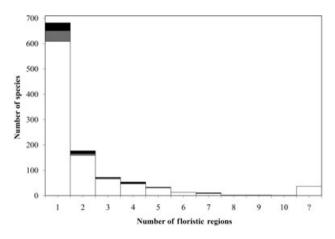


Figure 5. Greek endemic species occurring in 1–10 floristic regions: sexual species (open bar), apomictic species (black bar) and doubtful species (grey bar). The graph includes 1059 species with adequate data.

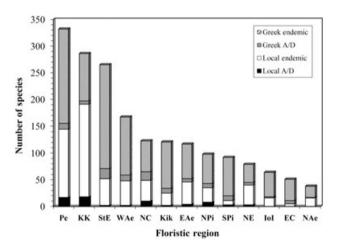


Figure 6. The distribution of the Greek endemic and local endemic species in floristic regions: Greek endemics, sexual (striped bar); Greek endemics, apomictic or doubtful (grey bar); local endemics, sexual (open bar); local endemics, apomictic or doubtful (black bar). The graph includes 1059 species with adequate data.

similarity coefficient. The differences in the resulting clustering were more marked among the two indices than among the three linkage methods, and the unweighted pair-group average (UPGMA) was finally selected as it is based on information about all intercluster pairs (Garson, 2008).

The analysis for all taxa (including subspecies and varieties) seems advantageous because the taxonomic position of several taxa is not clear and exclusion of endemics of infraspecific rank might screen cases of actual endemism. Nevertheless, the results were essentially similar when the analysis was performed at species level. Table 4 (unshaded part) shows the

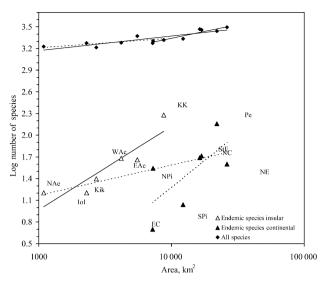


Figure 7. SARs: regression lines for all floristic regions (S); insular regions (Si); and continental regions (Sc). EARs: regression lines for all regions (E); insular regions (Ei); and continental regions (Ec). The analysis included 1059 endemic species with adequate data (doubtful and apomictic species included).

- S: y = 0.2009x 2.5687 (n = 13, $R^2 = 0.76353$, $F_s = 35.518$, P = 0.0001)
- Si: y = 1.1607x 2.5005 (n = 6, $R^2 = 0.83705$, $F_s = 20.548$, P = 0.01055)
- Sc: y = 1.5600x 4.9890 (n = 7, R² = 0.47862, F_s = 4.590, P = 0.08506)
- *E*: y = 0.4188x 0.0857 (*n* = 13, $R^2 = 0.16086$, *F*_s = 2.109, ns)
- *Ei*: y = 1.1536x 2.4915 (*n* = 6, R² = 0.81493, *F*_s = 17.613, *P* = 0.01373)
- Ec: y = 1.4853x 4.6609 (n = 7, R² = 0.46330, F_s = 4.316, P = 0.09235)

actual numbers of common Greek endemic taxa between regions and Table 5 demonstrates the similarity matrices used in clustering, the Preston index (unshaded part) and the Lance–Williams coefficient (shaded part). Both indices gave rather low similarity measures, apparently because of the presence of a large number of taxa restricted to only one region. The two distributional patterns (Fig. 8) are quite similar with certain features in common.

The most prominent of these features are: (1) the Central, South and East Aegean islands (Kik, KK, EAe) comprise a unit showing greater similarity among themselves than with any other region; (2) the Western Aegean (WAe) and the Northern Aegean (NAe) have greater affinity to the adjacent mainland areas rather than to the remainder of the Aegean islands; and (3) each continental region has greater similarity with its adjacent regions, the highest similarities shown in two pairs, Pe and StE in Southern

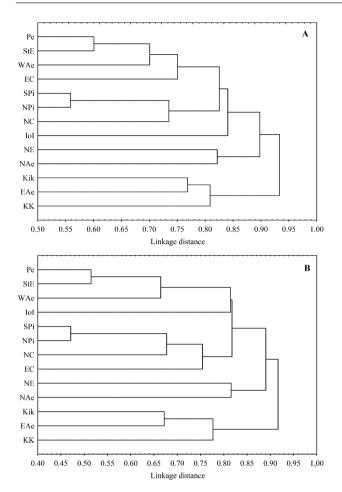


Figure 8. Dendrogram of the hierarchical cluster analysis of the distribution of Greek endemic taxa in floristic regions. The analysis included 1328 taxa with adequate data (doubtful taxa excluded). A, analysis with the Preston coefficient. B, analysis with the Lance–Williams coefficient.

Greece and SPi and NPi in Pindos. The main difference between the two distributional patterns is that the Preston index grouped NAe with the adjacent NE mainland and IoI with the adjacent regions of Western Greece rather than separate from all other regions; also, it grouped EC with the Southern Greece regions rather than with the more distant NE.

The similarity matrices (Table 5) highlight certain connections not apparent in the classification. The Ionian Islands (IoI) are closest to SPi and the other two regions with west-facing coastal parts, Pe and StE. Because of the proximity of the large island of Evvoia to the mainland, WAe firstly shares endemic species with StE and, secondly, with the other two regions with Aegean-facing coasts and islets, EC and Pe, but maintains a relation with Kik in the central Aegean. In the first instance, KK is closer to Kik, with which it comprises the 'Cardaegean', and, secondly, it is connected to EAe and Pe. There is also a closer connection of EAe with Kik than with the KK.

The endemic taxa occurring in only two regions were also examined (Table 4), as the existence of biregional endemics is a good indication of phytogeographical connections between regions. Table 4 shows a clearer picture of the relations between regions and underlines the above-noted affinities, such as the Pe-KK connection (22 biregional endemics, 12 of them from the islands of Kythira and Antikythira) and the EAe-Kik connection. Of the eight taxa endemic to Kik and EAe. two occur only on Ikaria in EAe, whereas the distribution of the other six in EAe includes at least one of the islands of Ikaria, Samos and Chios. Besides, all three WAe-EAe biregional endemics occur in the Ikaria-Samos area. The connection of NAe to NE is indicated by seven biregional endemics, all of which occur on the islands of Thasos and/or Samothraki.

ALTITUDINAL DISTRIBUTION

The occurrence of the Greek endemic species at each altitudinal zone (zones A to E, Table 1) shows that they can be found at all altitudes up to c. 3000 m (Mt Olympos summit at 2917 m). There is a rise at altitudes from 0 to 600 m and a gradual fall at higher altitudes, more marked above 2000 m (Fig. 9). It should, however, be kept in mind that such high altitudes represent a small percentage of the territory of Greece. This general altitudinal distribution pattern is observed in the local endemics of the floristic regions of Pe and KK (Fig. 9A). In the other island regions, except NAe (Fig. 9A), the fall is steeper at altitudes above 600 m, apparently because of the lack of high altitudes on most islands. However, in continental Greece, including StE, NE and EC (Fig. 9B), the endemics are concentrated at altitudes above 600 m. This pattern is more pronounced in the high-altitude mountainous areas of SPi, NPi and NC (Fig. 9B). On the one hand, although the endemics occur at all altitudes, the altitudinal range (Fig. 10) of each of them is not as wide: nearly half of them have a range of 0-600 m and a quarter of them are restricted to only one altitude or within a range of 200 m. On the other hand, a significant 31% has an altitudinal range of over 1000 m. The detailed distribution of endemics to altitudinal zones (Fig. 11A, main graph) shows that 35% of them occur in only one zone, 23% only at the thermo-Mediterranean zone (0-600 m) and 15% only at the mountain- and/or oro-Mediterranean zones (above 1500 m). However, a considerable number of species (23%) occur in three to five altitudinal zones. The altitudinal zone pattern is differentiated for local endemics in the floristic regions (Fig. 11B). In the island regions, there is a

	Pe	StE	WAe	IoI	SPi	NPi	EC	NC	NE	NAe	Kik	KK	EAe
Pe	423	188	85	52	49	35	32	30	22	10	46	72	36
StE	47	352	112	53	82	58	46	57	32	12	43	40	33
WAe	3	14	207	17	26	17	33	23	27	14	49	31	32
IoI	8	6	0	90	30	19	11	15	8	6	13	14	11
SPi	0	8	1	1	121	64	26	47	15	5	6	8	7
NPi	0	2	0	0	7	121	19	43	12	4	3	5	3
EC	2	2	3	0	0	0	74	32	21	8	6	7	8
NC	1	7	0	0	4	7	7	158	28	5	3	3	8
NE	0	0	3	0	1	0	1	2	106	14	9	6	7
NAe	0	0	1	0	0	0	0	0	7	46	8	6	11
Kik	3	2	11	0	0	0	0	0	0	1	157	66	50
KK	22	1	0	1	0	0	0	0	0	0	23	371	51
EAe	0	0	3	0	0	0	0	0	0	3	8	11	148

Table 4. Common endemic taxa between floristic regions in absolute numbers (unshaded area) and distribution of biregional endemics (shaded area)

The bold type indicates the Greek endemic taxa in each region. The analysis included 1328 taxa with adequate data (doubtful taxa were excluded).

Table 5. Dissimilarity coefficients between pairs of floristic regions: Preston z (unshaded area); Lance–Williams coefficient (shaded area)

	Pe	StE	WAe	IoI	SPi	NPi	EC	NC	NE	NAe	Kik	KK	EAe
Pe	0.00	0.60	0.76	0.74	0.81	0.87	0.83	0.91	0.91	0.92	0.86	0.87	0.89
StE	0.51	0.00	0.65	0.72	0.63	0.76	0.70	0.81	0.86	0.90	0.86	0.92	0.89
WAe	0.73	0.60	0.00	0.91	0.87	0.91	0.77	0.91	0.86	0.87	0.79	0.92	0.86
IoI	0.80	0.76	0.89	0.00	0.77	0.86	0.90	0.90	0.94	0.93	0.92	0.94	0.93
SPi	0.82	0.65	0.84	0.72	0.00	0.56	0.78	0.73	0.91	0.95	0.97	0.97	0.97
NPi	0.87	0.75	0.90	0.82	0.47	0.00	0.84	0.75	0.92	0.95	0.99	0.98	0.99
EC	0.87	0.78	0.77	0.87	0.73	0.81	0.00	0.76	0.82	0.90	0.96	0.96	0.94
NC	0.90	0.78	0.87	0.88	0.66	0.69	0.72	0.00	0.84	0.95	0.99	0.99	0.96
NE	0.92	0.86	0.83	0.92	0.87	0.89	0.77	0.79	0.00	0.84	0.95	0.97	0.96
NAe	0.96	0.94	0.89	0.91	0.94	0.95	0.87	0.95	0.82	0.00	0.92	0.95	0.89
Kik	0.88	0.83	0.73	0.89	0.96	0.98	0.95	0.98	0.93	0.92	0.00	0.77	0.74
KK	0.82	0.84	0.89	0.94	0.97	0.98	0.97	0.99	0.97	0.97	0.75	0.00	0.83
EAe	0.87	0.87	0.82	0.91	0.95	0.98	0.93	0.95	0.94	0.89	0.67	0.80	0.00

The analysis included 1328 taxa with adequate data (doubtful taxa were excluded).

predominance of local endemics restricted to or occurring at the thermo-Mediterranean zone, which decreases as the coverage in high mountains increases (e.g. KK and NAe). Conversely, most of the local endemics of the continental regions are restricted to zones above 1000 or 1500 m.

BIOLOGY

Life form is the functional attribute investigated in the endemic species (Table 6). The hemicryptophytes (93% scapose, caespitose or rosette-forming perennials and 7% biennials) are by far the most frequent, followed by the chamaephytes (83% subshrubs or dwarf shrubs, 15% mat-forming or prostrate and 1% succulent). The proportions of geophytes and annuals (therophytes) are significantly lower and only 1% of the endemic species are phanerophytes (mostly nanophanerophytes).

In Greece, as shown by the floras of various areas (Table 6, Voliotis, 1982; Vogiatzakis, Griffiths & Mannion, 2003), the life form spectra typically shift from a predominance of annuals at lower altitudes and southern regions with higher temperatures and extended drought periods to a predominance of hemicryptophytes and chamaephytes at higher altitudes and northern regions with lower temperatures and higher rainfall. Compared with this trend for the total

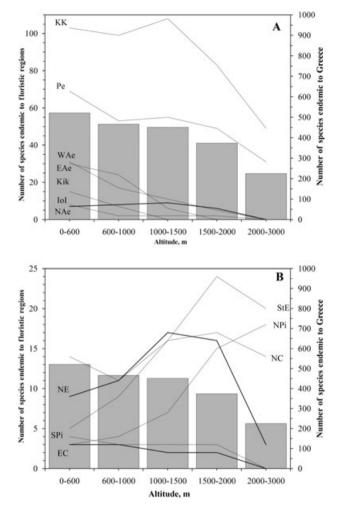


Figure 9. Occurrence of the Greek endemic species in altitudinal zones (all species occurring at the indicated range are included) in Greece (bars, secondary y axis) and of local endemics in each floristic region (lines, primary y axis). A, insular regions. B, continental regions. The analysis included 860 species with adequate data (doubtful and apomictic species excluded). Altitudinal zones are defined in Table 1.

flora, the life form spectrum of the endemics, with a predominance of perennial hemicryptophytes and chamaephytes and low proportions of annuals, is closer to the spectra for high mountains, with the exception of the usually high proportions of geophytes and chamaephytes among the endemics. A similar trend is observed in Cyprus where, for the total flora, the proportion of annuals is higher and the proportion of hemicryptophytes is lower than for the endemic flora (Table 6, Hadjikyriakou, 1997). The obligate chasmophytes (75% endemic) of Kriti are mainly chamaephytes and hemicryptophytes as opposed to the general chasmophytic flora which has an increased proportion of annuals (Table 6, Kypriotakis, 1997). In

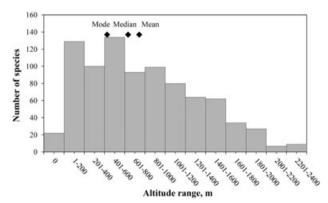


Figure 10. Frequency classes of the altitude range of the Greek endemic species. The analysis included 860 species with adequate data (doubtful and apomictic species excluded).

the regional life form spectra of the endemics (Fig. 11B) it is shown that southern warmer regions (e.g. EAe) have higher proportions of annuals and northern regions (e.g. NC) have higher proportions of hemicryptophytes. This indicates that the trend of the total flora is repeated in the endemic flora, although the percentages differ. Pe and StE, with high mountains, extensive coastlines and offshore islets, are close to the general pattern for the endemics. In order to investigate whether the life form of the endemics is related to their altitude range, and therefore to bioclimate, the life form spectra for plants of each altitudinal zone were plotted (Fig. 11A, inserted graph). There is a trend for a decrease of annuals and geophytes and an increase of hemicryptophytes in plants occurring at or restricted to the higher altitudes, but the life form spectra of the endemics still maintain their differences from the total flora spectra. The other life forms maintain more or less the same pattern.

CONSERVATION STATUS

The main sources for the conservation status of the Greek endemics are the *Red Data Book of Rare and Threatened Plants of Greece* (Phitos *et al.*, 1995) and the IUCN-WCMC database (IUCN-WCMC, 1997), in which 873 taxa in total were classified according to old IUCN categories. A preliminary classification in new IUCN categories (1994 version) was attempted for the plants of Southern Greece, including 189 endemic taxa (Georghiou & Delipetrou, 2001), and for 50 taxa by the Mediterranean Island Plant Specialist Group (De Montmollin & Strahm, 2005). Valid literature sources (e.g. Iatrou, 1986; Trigas, 2003) and recent unpublished field work provide additional information on the conservation status or rarity of 321 endemic taxa.

The compiled information on the conservation status of the endemics is presented in Figure 12, with

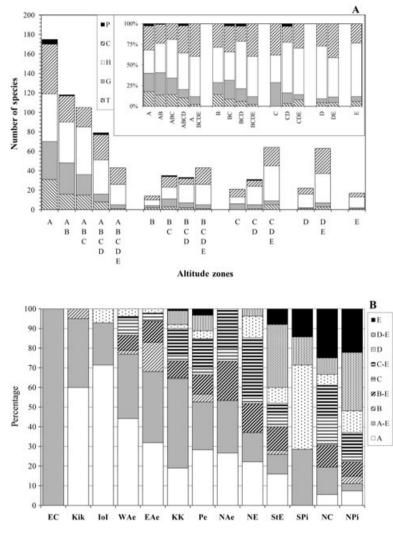


Figure 11. A, altitudinal distribution in zones (only species restricted at the indicated zone are included) of the Greek endemic species and their life forms in counts (main graph) and percentages (inserted graph). T, annuals (Therophytes); G, geophytes; H, hemicryptophytes; C, chamaephytes; P, phanerophytes. B, altitudinal distribution in zones of the local endemics in each floristic region (A, B, C, D, E represent species restricted to each zone; A–E, B–E, C–E, D–E represent species occurring in more than one zone in the indicated range). The analysis included 860 species with adequate data (doubtful and apomictic species excluded). Altitudinal zones are defined in Table 1.

the plants characterized according to the old (Lucas & Synge, 1978) or the new (IUCN, 2001) IUCN threat categories, depending on the available data. There are 253 (18% of the total) threatened (critically endangered, endangered or vulnerable) and seven extinct or doubtfully extinct Greek endemic taxa. Another 369 taxa (26% of the total) have been characterized as indeterminate or rare and, in our experience, these usually turn out to be either vulnerable (VU) or near-threatened (NT). However, a significant 19% of the plants are apparently of least concern (LC).

There are few known cases of extinction in the endemic Greek flora. Two species are in all probability extinct. *Ammi topalii* Beauverd, known only from the type specimen collected in 1935 (Rechinger, 1961) was not found in a recent search of its location and may have disappeared as a result of the change in land use (Iatrou & Trigas, 1996; Trigas, 2003). *Geocaryum bornmuelleri* (Wolff) Engstr., also known from a single gathering on the island of Thasos in 1891 (Greuter, 1995), has also not been refound (Strid & Tan, 1997). The doubtfully extinct taxa are *Brassica cadmea* Heldr. ex O.E.Schulz, *Centaurea tuntasia* Heldr. ex Halácsy, *Cerastium illyricum* Ard. ssp. *crinitum* (Lonsing) P.D.Sell & Whitehead, *Geocaryum divaricatum* (Boiss. & Orph.) Engstr. and *Tetragonolobus wiedemannii* Boiss. Most of them are inadequately known, and the last three are of doubtful taxonomic

	Life	form (%	6)†			
Area	Т	G	Н	Ch	Р	
Greek endemics*	11	17	44	27	1	Chloris database
NC	7	14	57	21	1	Chloris database
SPi	8	24	45	23	1	Chloris database
NE	9	16	52	22	1	Chloris database
NPi	11	15	55	20	0	Chloris database
WAe	12	18	43	27	1	Chloris database
Pe	12	14	44	28	1	Chloris database
StE	12	17	44	24	2	Chloris database
EC	16	14	52	18	0	Chloris database
KK	17	19	31	31	3	Chloris database
IoI	18	25	34	21	2	Chloris database
NAe	19	14	49	16	3	Chloris database
Kik	19	27	34	17	3	Chloris database
EAe	21	27	30	19	4	Chloris database
Vrontous Mt (1849 m, NE)	13	12	54	8	12	Voliotis, 1977
Voras Mt (2524 m, NC)	14	11	57	7	10	Voliotis, 1979
Vermion Mt (2052 m, NC)	15	14	51	10	10	Chochliouros, 2005
Vermion 500–1000 m	35	16	26	6	17	Chochliouros, 2005
Vermion 1000–1650 m	18	16	37	9	20	Chochliouros, 2005
Vermion 1650–2052 m	4	9	66	17	4	Chochliouros, 2005
Menoikio Mt (1963 m, NE)	20	6	54	10	10	Karagiannakidou, 1991
Kyllini Mt (2376 m, Pe)	24	13	43	10	10	Dimopoulos, 1993
Kyllini 0–600 m	39	12	31	5	13	Dimopoulos, 1993
Kyllini 2000–2376 m	10	9	55	23	3	Dimopoulos, 1993
Cholomon Mt (1165 m, NE)	26	15	32	12	15	Voliotis, 1967
Central Evvoia Island (WAe)	29	8	43	10	4	Phitos, 1960
Vertiskos Mt (1103 m, NE)	30	10	42	5	11	Pavlides, 1982
Sithonia peninsula (NE)	42	9	30	8	9	Pavlides, 1976
Samos Island (EAe)	42	15	24	10	9	Christodoulakis, 1986
Cretan area (KK)	42	15	21	14	6	Jahn & Schönfelder, 1995
Kriti – chasmophytes	31	11	22	26	10	Kypriotakis, 1997
Kriti – obligate chasmophytes	0	3	30	60	7	Kypriotakis, 1997
Geraneia Mt (1269 m, StE)	43	14	26	11	6	Constantinidis, 1997
Skiathos Island (WAe)	45	12	25	7	8	Economidou, 1969
Skopelos Island (WAe)	47	13	19	10	9	Economidou, 1973
Kythira Island (Pe)	52	12	17	11	8	Yannitsaros, 1969
Nisyros Island (EAe)	55		17	9	10	Papatsou, 1975
Arkoi–Leipsoi islet complex (EAe)	59	15	15	6	5	Panitsa, 1997
Cyprus	49	17	21	5	7	Hadjikyriakou, 1997; CyprusFlora database
Cyprus endemics	11	23	40	22	4	Hadjikyriakou, 1997; CyprusFlora database

Table 6. Life form spectra in floras of Greek areas

*The analysis included 935 species with adequate data (doubtful and apomictic species excluded).

†T, annuals (Therophytes); G, geophytes; H, hemicryptophytes; C, chamaephytes; P, phanerophytes.

status (Routsi, 1993, Greuter, 1995; Strid & Tan, 1997, 2002). Some other allegedly extinct endemics (Phitos *et al.*, 1995; Tan & Strid, 1997), *Alkanna sartoriana* Boiss. & Heldr. (Vassiliadis, 1996) and *Astragalus maniaticus* Kit Tan & Strid (Tan & Iatrou, 2001), have been rediscovered. According to the above, at the worst, only 0.5% of the endemic taxa are extinct. However, 35% of the endemics have not been evaluated at all (NE) or are insufficiently known (DD), including at least 35 taxa that have not been collected or looked for, for the last 60 to > 100 years.

DISCUSSION

The floristic analysis of the endemic taxa highlighted certain families which are important at Mediterra-

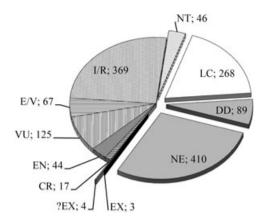


Figure 12. Conservation status of the Greek endemic taxa (including doubtful and apomictic taxa). New IUCN categories (IUCN, 2001): EX, extinct; ?EX, doubtfully extinct; CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern; DD, data deficient; NE, not evaluated. Old IUCN categories (Lucas & Synge, 1978): E, endangered; V, vulnerable; R, rare; I, indeterminate.

nean level. Asteraceae have an excess of endemic genera in East Asia and North America (Qian. 2001). Caryophyllaceae show active endemism in Greece (Trigas, Iatrou & Karetsos, 2007) and, with Brassicaceae, have large concentrations of genera in the Mediterranean basin (Heywood et al., 2007). The Mediterranean basin is a centre of diversification for Lamiaceae (Heywood et al., 2007) and the evolutionary centre of all the Greek genera of Campanulaceae (Eddie et al., 2003). The 10-12 families with the highest numbers of endemic species more or less fall within the richest families of the total Greek flora (as indicated by the studied floras of several areas), a trend also observed in other Mediterranean type climate provinces (Beard, Chapman & Gioia, 2000). A striking difference between the total and endemic Greek flora is seen in Poaceae and Fabaceae which, along with Asteraceae, invariably figure among the three richest and most diverse families in Greece and in the Mediterranean (Blondel & Aronson, 1995; Maxted & Bennett, 2001), but rank lower in both absolute number of endemics and degree of endemism (6 and 10%, respectively) in Greece. Also, the 10-12 families richest in endemics in Greece coincide with those in neighbouring Cyprus (Hadjikyriakou, 1997) and Turkey (Davis, 1965–1986). The main differences between the three countries are noted in Fabaceae (higher rank in Turkey), Campanulaceae (higher rank in Greece) and Crassulaceae (higher rank in Cyprus).

The total species/genus ratio (4.4) is somewhat lower than the ratio for the total flora (5.5; Strid & Tan, 1997) and medium compared with the 3.0–9.0 for the floras of other Mediterranean-type climate regions (Blondel & Aronson, 1995; Fenner *et al.*, 1997). The total Greek flora is characterized by a majority of small-sized genera, with at least 473 genera represented by only one species (Strid & Tan, 1997), and this trend is repeated in the endemic flora. The high endemism of certain genera, such as *Centaurea*, which comprises both relict and neoendemic taxa (Georgiadis, 1980; Routsi, 1993), and *Allium* may indicate recent speciation (Fenner *et al.*, 1997).

The distribution of the endemics is characterized by a high frequency of narrowly distributed species (Fig. 5) and by a north-to-south and a west-to-east increase of local endemism (Fig. 6). The first result supports the notion that increased diversity is related to high incidence of local combined with regional endemism in Mediterranean basin floras (Greuter, 1991, 1995). The second result confirms previous reports, based on subtotals of the endemic taxa, that endemism in the mountain flora increases southwards, with taxa tending to be more narrowly distributed and reproductively isolated (Strid, 1986, 1993), and that in the genus Centaurea there is an east-towest reduction of the number of endemics, with the western taxa having evolved more recently (Georgiadis, 1980; Georgiadis, Iatrou & Georgiou, 1986). Both Bykov's indices for floristic regions (Fig. 2) and the counts of endemic species as a function of area (Fig. 7) are consistent with the above and show the island regions to be centres of endemism.

The slope of the SAR for the total flora (z = 0.20) of the floristic regions was at the margin of the range (0.1-0.2) of z expected for the flora of mainland intraprovincial (nested sampling, sensu Rosenzweig, 1995, 2004) SARs or SARs expected for mainland areas larger than 10 km² (Crawley & Harral, 2001) or of non-isolated islands (McArthur & Wilson, 1967). Such SARs are interpreted as the result of accumulation of habitat heterogeneity within a region/province (Rosenzweig, 1995), implying that the floristic regions of Greece constitute parts of the same province. However, as the total flora SAR has not been constructed from a nested design, and as some floristic regions are continental and some islands (i.e. with different underlying processes for biodiversity), any such theoretical interpretation is precarious. Indeed, the SAR slope and explanatory value change when the model is applied to continental and island regions separately and has lower explanatory value for island regions, indicating the greater involvement of other factors; for example, habitat diversity and isolation (Yeakley & Weishampel, 2000; Triantis et al., 2003; Field et al., 2008). For instance, the longer isolated KK has a relatively low total species number despite the size and habitat diversity of the island of Kriti.

In all cases, EARs had slopes steeper than those of the SARs for the total flora as predicted for log–log models by Harte & Kinzig (1997) and also confirmed in several cases either for islands (Roos et al., 2004: Triantis, Mylonas & Whittaker, 2008) or continental nested areas (Ulrich, 2005), and even in the contiguous US (Harte & Kinzig, 1997). The steep curves indicate a larger increase in the number of endemics than the total species richness for the same areas and may partly reflect the large number of smallrange species (Reid, 1992). The steep single-island endemic curves have been interpreted as an evolutionary dynamics metric of speciation (Triantis et al., 2008; Whittaker, Triantis & Ladle, 2008), but our study does not have the detail needed for such conclusions. On the whole, the results of the EARs indicate that area is a good predictor of endemism in the floristic regions, especially in the island regions, but is not adequate alone, and other variables such as history and isolation are expected to play a significant role (Yeakley & Weishampel, 2000; Whittaker, Willis & Field, 2001). The higher concentration of endemics in the island regions is a trait also observed at the scale of the Med-Checklist territories (Greuter, 1995).

The analysis of the distribution of the endemics by similarity coefficients and hierarchical classification can be a tool for the study of palaeogeography and biogeography in Greece. The pattern of affinities of WAe to the other regions is similar to the phytogeographical connections of Evvoia that arose by comparisons of the total floras (Trigas, Iatrou & Panitsa, 2008) and the similarly of Pe to StE was also found for mountain taxa (Strid, 1993). The KK-Pe affinity, commented upon by Greuter (1975), may reflect the connection of West Kriti with Peloponnisos until the late Miocene (Dermitzakis & Papanikolaou, 1981), possible Pliocene connections of West Kriti with the island of Antikythira (Vardinoyannis, 1994) and possible Kriti to Kythira colonization later than 4 Mya (Parmakelis et al., 2006). The Kik-EAe affinity and biregional endemics agree with: the connection of the EAe islands of Ikaria and Chios to the Cyclades with which they most probably formed a continuous landmass until the lower Pliocene (map in Simaiakis & Mylonas, 2006); the possible Evvoia (WAe)-Attiki (StE)-Cyclades (Kik) connection to Asia Minor through the islands of Chios and Samos during the Tortonian and Messinian (Dermitzakis & Papanikolaou, 1981); and the Kik-EAe bridge during the Pleistocene (map in Poulakakis et al., 2005). The NAe-NE affinity and biregional endemics agree with the connection of Thasos and Samothraki to the mainland until the Middle Pleistocene and their early separation from the other Aegean islands (Dermitzakis & Papanikolaou, 1981; Durand et al., 1999). A coupling of the detailed distribution with phylogenetic relationships of the endemics would prove enlightening.

On the whole, although the Lance–Williams coefficient resulted in slightly higher similarity measures, the Preston index performed better in terms of interpretation. The Lance–Williams coefficient is more sensitive to the large disparity in the total number of endemics in each region and the Preston index was also considered preferable to the Jaccard index in the numerical analysis of the floras of Aegean Islands and the adjacent Asia regions (Carlström, 1987).

The altitudinal distribution of the endemics reveals that they occur at all altitudes, but there is a concentration in the thermo-Mediterranean zone below 600 m, particularly in the island regions. There is, however, a clear positive relationship of the number of species with altitude, such as found in endemics of the southern Iberian peninsula (Giménez et al., 2004), Bolivia (Kessler, 2000) and South African fynbos (McDonald & Cowling, 1995), in the continental floristic regions, where mountain isolation has promoted endemism (Strid & Papanikolaou, 1985). A significant number of species transgresses the altitudinal zones, and hence bioclimates, apparently being adapted to a wider range of environments. A similar trend has been found in Corsica, in contrast to south-east France, and has been considered as a pattern of widening ecological niche in island environments (Médail & Verlague, 1997). In KK, where both island and mountain isolation have played a role in plant endemism (Legakis & Kypriotakis, 1994, also see Introduction), 43% of the local endemics occur in the zones from below 600 m to above 1000 m, but there is also a significant proportion (20%) restricted to the zones above 1000 m.

Life form, the fundamental characteristic of a plant (Barboni et al., 2004), is an attribute related to bioclimate and altitudinal distribution (Raunkiaer, 1934; Gentry, 1988; Danin & Orshan, 1990; Verlague et al., 2001). The life form spectra of the Greek endemics, although following the trends of the total Greek flora, maintain at all altitudinal zones and in all floristic regions the high percentages of hemicryptophytes typical of mountainous regions. These spectra, although reminiscent of the theory that Aegean endemics are mainly mountain endemics with distribution areas older than the current land/sea distribution (Rechinger, 1965), are related to but not adequately explained by the bioclimate or altitudinal zone of the endemic plants. High proportions of hemicryptophytes among the Greek endemics have been observed even in the floras of small islets (Vallianatou, 2005). In New Zealand, the endemic flora life form spectra also resemble those of the alpine flora (McGlone, Duncan & Heenan, 2001) and the prominence of woody endemics (including shrubs and subshrubs) was related to dispersal ability and habitat and hence to the trend towards reduced dispersability and the shift from herbaceous annuals to woody

perennials found in isolated island populations (Carlquist, 1974, 2009, Böhle, Hilger & Martin, 1996; Cody & McOverton, 1996). This trend might apply to island or mountain top endemics.

The difference in the life form spectra between the endemic and the total flora is partly related to the differences in family composition, although again the endemic flora follows the total flora trend. For example, Fabaceae have a high proportion of annuals in both in the total (c. 40%, see literature in Table 6) and the endemic flora (27%), but they are represented by many fewer species in the endemic flora than Asteraceae, which in contrast have a high proportion of hemicryptophytes in both the total (see literature in Table 6) and the endemic flora (80%). The flora of Cataluña, which has a high proportion of endemic members of Fabaceae, also has an increased proportion of chamaephytic members of Fabaceae compared with other Mediterranean area floras (Blondel & Aronson, 1995).

In Mediterranean-type climate regions, high proportions of herbaceous perennials and soft shrubs characterize the endemic floras of Sardinia (Bacchetta, Iiriti & Pontecorvo, 2004), south-eastern Spain (Melendo et al., 2003), California and Italy (Beard et al., 2000), whereas woody shrubs and herbaceous perennials characterize the endemic floras south-west Australia and the Cape region of South Africa (Beard et al., 2000; Ojeda *et al.*, 2001). These life form spectra are at least partly interpreted as a result of habitat specialization to infertile and rocky substrata. Life form is expected to be an attribute related to the habitat of the endemics and is indicative of their ecological strategy (Grime, 1979; Grime, Hodgson & Hunt, 1988) and of the degree of disturbance (Leishman & Westoby, 1992; McIntyre, Lavorel & Tremont, 1995; Médail et al., 1998). Endemic species are known to be stress tolerant, occupying more infertile, steeper and rockier habitats with reduced competition than more common plants (Médail & Verlaque, 1997; Desmet & Cowling, 1999; Ojeda et al., 2001; Lavergne et al., 2004) and predominance of stress-tolerance strategies was found in the endemics of Evvoia (Trigas et al., 2008). Regarding the habitat of the Greek endemics, a preliminary investigation (data not shown) and the literature (Rechinger & Rechinger-Moser, 1951; Snogerup, 1985; Strid & Papanikolaou, 1985; Strid & Tan, 1997; Trigas et al., 2008) indicate that the majority of the endemics are inhabitants of rocks, cliffs and screes (70-80% hemicryptophytes and chamaephytes) or, less often, of dry, poor soils with phrygana (40% geophytes and 40% hemicryptophytes and chamaephytes), garrigue or grassland. These habitats are most often characterized by low productivity and intense drought stress combined with low- to high-intensity unpredictable yet recurrent or even continuous, anthropogenic (e.g.

grazing) or natural (e.g. wind) disturbance (sensu Noble & Slatver, 1980). This is the case in small islets. cliffs and rocks, grazed phrygana and grassland, fireprone habitats affected by wind and salt spray. In fact, habitats such as coastal rocks may promote speciation processes (Crespo, De la Torre & Costa, 2003). Perennation by roots or stress-tolerant leaves and vegetative reproduction are characters associated with a stresstolerant strategy (Grime et al., 1988). The taproots and ligneous underground or slightly above ground parts of hemicryptophytes and chamaephytes may effectively withstand and help in the recovery from wind blowdowns. Indeed, the cliff floras are characterized by slow-growing, desiccation tolerant or avoidant, perennial plants (Larson, Matthes & Kelly, 2000). In contrast, medium grazing, frequent in phrygana habitats, favours geophytes and hemicryptophytes (McIntyre et al., 1995; Noy-Meir & Oron, 2001).

Do the predominant life forms of the endemics represent adaptations to the present ecological conditions or are they related to phylogenetic restrictions, evolved in plants before the onset of the Mediterranean climate? The Mediterranean islands have functioned as museums for elements of former vegetation that have been replaced elsewhere, but in the Aegean islands there are many cases of post-Pleistocene neoendemics (Snogerup, 1967a, b, Strid, 1970; Bothmer, 1974; Thompson, 2005), and neoendemics are also prominent in the continental flora (seed introduction). The life form pattern of the endemics cannot be explained adequately by altitudinal distribution or family composition, but it seems indicative of their habitat and adaptive strategy. It could also be surmised that it is related to speciation processes. Chasmophytism is supposed to be a secondary development for certain elements that found refuge in the Aegean cliffs (Snogerup, 1985) and lignification can develop by island isolation (review in Whittaker & Fernández-Palacios, 2007). Moreover, longevity is a trait connected to a local persistence syndrome considered as a key feature for the ecology and long-term viability of rare endemics (García & Regino, 2003; Lavergne et al., 2004).

The overview of the conservation status of the Greek endemics indicates that more than 40% of the taxa are threatened or near threatened but only 0.5% may be extinct. In many cases, the criteria for the threat are based on the small area of occurrence or extent of occupancy which is an intrinsic characteristic rather than a result of distribution area reduction caused by anthropogenic threats. A similar situation occurs in Cyprus, where 32% of the endemics are threatened and none extinct and the restricted distribution is the threat criterion for 60% of the threatened endemics (Tsintides *et al.*, 2007). Rarity can mean vulnerability, but when, as in the case of

Greece, either relic species or newly evolving neoendemics are involved, rarity can also be related to endemism (Ricklefs, 1995). This is characteristic of the floras of the Mediterranean basin, where species diversity is positively correlated to endemism and rarity and, despite the large number of rare species, the confirmed cases of extinction amount to a mere 0.11% of the endemic Mediterranean element (Greuter, 1995). In Greece, many rare endemics also inhabit inaccessible habitats and are minimally affected by anthropogenic threats. However, grazing, a human activity widespread in Greece and most often included in the main threats of rare species, may have actually pushed certain species to inaccesible cliffs. Nevertheless, some endemics seem to tolerate grazing (Bergmeier, 1998). Moreover, controlled grazing by maintaining a diverse landscape may increase plant diversity and favour certain plants linked to disturbance (Verdú, Crespo & Galante, 2000).

However hopeful the above facts may seem, the ever-increasing land-use changes in coastal areas pose a significant threat, especially to island endemics and to coastal and wetland species. Sand dune inhabitants with limited distributions such as *Silene ammophila* Boiss. & Heldr. (endemic to KK) are under immediate threat. Finally, global climate change is an impending threat, especially for the mountain endemics with restricted altitudinal distribution.

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