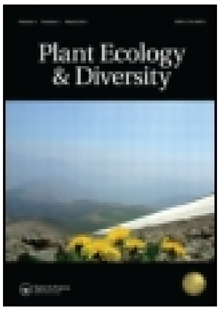

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Ecological factors driving plant species diversity in the South Aegean Volcanic Arc and other central Aegean islands

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Ecological factors driving plant species diversity in the South Aegean Volcanic Arc and other central Aegean islands

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Background: The South Aegean Volcanic Arc (SAVA), one of the most notable geological structures of the Mediterranean Sea, is floristically well known. Nevertheless, the factors that contribute to shaping the plant species richness of the SAVA remain unclear.
Aims: To investigate the factors that affect plant species richness and identify plant diversity hotspots in the SAVA and other central Aegean islands.
Methods: We used stepwise multiple regression to test the relationship between a number of environmental factors and plant species richness in the SAVA, as well as the residuals from the species–area linear regressions of native, Greek and Cycladian endemic taxa as indicators of relative species richness.
Results: The area was confirmed to be the most powerful single explanatory variable of island species richness, while geodiversity, maximum elevation and mean annual precipitation explained a large proportion of variance for almost all the species richness measures. Anafi, Amorgos and Folegandros were found to be endemic plant diversity hotspots.
Conclusions: We have demonstrated that geodiversity is an important factor in shaping plant species diversity in the Cyclades, while mean annual precipitation, human population density and maximum elevation were significant predictors of the Greek endemics present in the Cyclades. Finally, Anafi was found to be a plant diversity hotspot in the South Aegean Sea.

Keywords: Aegean archipelago; endemism; environmental diversity; geodiversity; human impact; island species–area relationship; species richness; South Aegean Volcanic Arc

Introduction

The Mediterranean biome has been identified as an ecological hotspot (Médail and Quézel 1997; Myers et al. 2000), and the five Mediterranean-type climate regions of the world are renowned for their high levels of plant richness and endemism, exceeding the combined flora of tropical Africa and Asia (Cowling et al. 1996). The Mediterranean biome, although representing only 2% of the world's surface area, contains 20% of the world's plant species (Médail and Quézel 1997). Moreover, the European area of the Mediterranean Basin, rich in islands, is one of the world's major centres of plant diversity, 10% of all known higher plants being found there (Médail and Quézel 1997). Within the Mediterranean Basin Médail and Quézel (1999) have recognised 10 areas as biodiversity hotspots, including central and southern Greece, in addition to Kriti (Crete).

A considerable number of the plant species worldwide are associated with islands (Kreft et al. 2008), although islands have generally been considered less diverse than their adjacent mainland counterparts (Whittaker and Fernández-Palacios 2007). On the other hand, according to Barthlott et al. (2005) five of the 20 global centres of plant species richness represent islands or include island areas, and nine of the 25 global biodiversity hotspots encompass islands or archipelagos (Myers et al. 2000).

The Aegean Sea has long attracted the attention of biogeographers (Turill 1929; Rechinger 1943; Greuter 1970; Runemark 1970; Strid 1996). The entire Aegean region is characterised by high levels of diversity and endemism (Strid 1996) and has a complex palaeogeographical history. The present day Aegean archipelago has been shaped by the different effects of tectonism, volcanism and eustatism (for a detailed review of the palaeogeographical history of the Aegean region, see Sfenthourakis (1996) and Lykousis (2009)). The majority of the Aegean islands can be divided into two groups, those lying on the European shelf off the eastern coast of Greece and those associated with the seaboard of Asia Minor (Foufopoulos and Ives 1999). A third group, the Cyclades, forms a central independent shelf that has been separated from Europe since the Middle Pleistocene era (Sondaar 1971; Sondaar et al. 1986). Since the peak of the Winsconsin–Würm glaciation, global sea levels have risen by 120–130 m, creating out of what was once a continuous land and coastal landscape the present island clusters of the Aegean Sea (van Andel and Shackleton 1982; Dermitzakis and Sondaar 1985; Papageorgiou et al. 1990; Pirazzoli 1991). Between 350 and 250 Ka BP, the subaerial land was extended, the sea was restricted and almost 50–60% of the present Aegean Sea became land, with extensive drainage systems, delta plains and large

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lakes (Lykousis 2009). At 18 Ka BP many of the Cycladic islands were welded together to form a single large unit, probably separated from the mainland by a very shallow strait 10 km wide, but may possibly have remained attached (van Andel and Shackleton 1982). The Late Palaeolithic geography of the central Aegean is characterised by extensive coastal lowlands and a large Cycladic land area or peninsula (Lambeck 1996). By 9 Ka BP, the degree of coastal lowland was only slightly greater than today, and the Cycladic land had become fragmented (Lambeck 1996).

The South Aegean Volcanic Arc (SAVA; Figure 1) is one of the most significant geological structures in the Mediterranean, as it is located on the edge of two tectonic plates, the African plate and the Aegean–Anatolian microplate. The SAVA is floristically relatively well-known (Hansen 1971; Papatsou 1974; Raus 1986, 1988, 2012; Burton 1991; Vallianatou 2005; Kougioumoutzis et al. 2012a, 2012b). The vast majority of the SAVA is located in the southern Cycladic islands, stretching from Sousaki in the west to Nisyros in the east. It is the result of the subduction of the African plate beneath the Aegean–Anatolian microplate (Anastasakis and Piper 2005), and is located about 130–150 km above the seismically defined Benioff zone (Makropoulos and Burton 1984).

The Cyclades are floristically impoverished (Phitos et al. 1995). According to Snogerup et al. (2006) the Cyclades have their main floristic connections towards the west, in other words to the European mainland, and the floristic division between Europe and Asia ('Rechinger's line') falls between the Cyclades and the eastern Aegean islands. The Cyclades host 1640 taxa (Tan and Iatrou 2001), 157 of which are considered endemics and represent 9.4% of the flora (Georghiou and Delipetrou 2010). According to these authors the Cyclades demonstrate lower than normal endemism, as expected from their size. However, their degree of endemism is above average (ca. 8%) in the overall context of Mediterranean islands (Médail and Quézel 1997).

A number of studies have suggested that the distributional patterns of the animal and plant groups in the Aegean Sea may reflect palaeogeographical patterns or historical events (Comes et al. 2008 and references therein). Biogeographical and ecological factors determining the total and endemic plant species richness of eastern and southern Aegean islands and islets have been investigated fairly recently by Panitsa et al. (2006, 2010) and Kagiampaki et al. (2011). In addition, Kallimanis et al. (2010, 2011) have examined a dataset of 201 Aegean islands and islets covering all Aegean phytogeographical regions, investigating the factors affecting total and endemic plant species richness. To our knowledge there has been no study specifically investigating the relationship between Cycladic plant species richness and island area

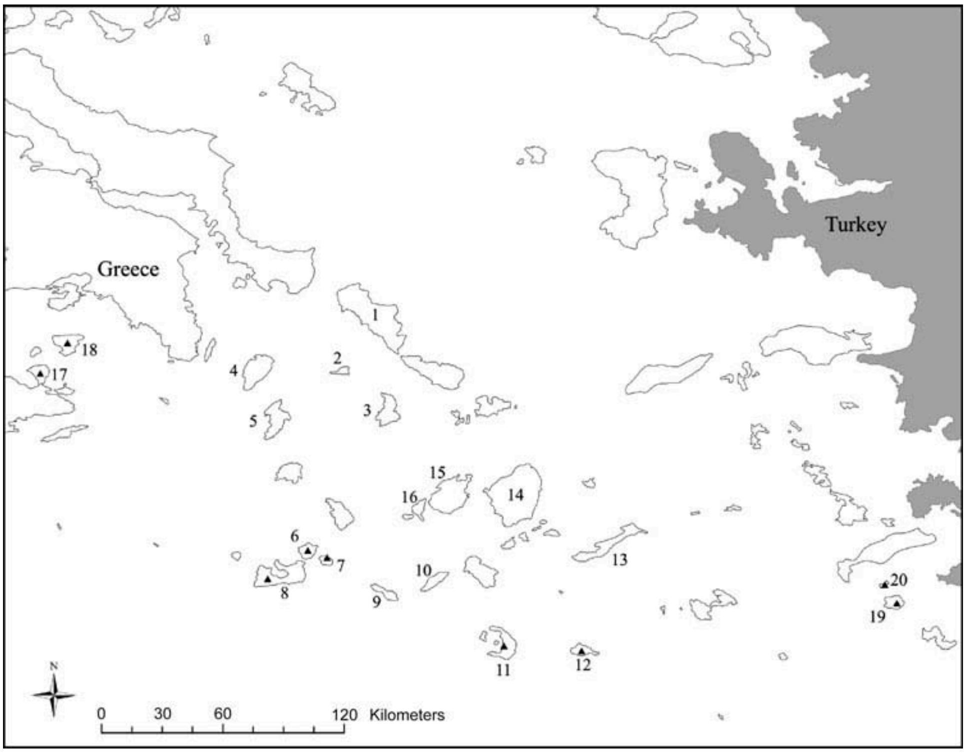

Figure 1. The Cycladic Islands included in the present study (nos. 1–16, Dataset 1), as well as the rest of the members of the SAVA (nos. 17–20). Numbers correspond to the islands as follows: 1. Andros (And), 2. Giaros (Gi), 3. Syros (Syr), 4. Kythnos (Kyt), 5. Serifos (Ser), 6. Kimolos (Kim), 7. Polyaegos (Pol), 8. Milos (Mi), 9. Folegandros (Fol), 10. Sikinos (Sik), 11. Santorini (Sant), 12. Anafi (An), 13. Amorgos (Am), 14. Naxos (Na), 15. Paros (Pa), 16. Antiparos (Antp), 17. Methana Peninsula, 18. Aegina, 19. Nisyros, 20. Gyali. Black triangles indicate the islands comprising the SAVA.

or other physiographical, climatological or geological parameters. Moreover, the role of climate, a very important factor in global patterns of plant species richness (Francis and Currie 2003), has never been examined in the Aegean archipelago. Similarly, the effect of geodiversity and human disturbance in shaping the assembly of Aegean plant taxa has not so far been examined using stepwise multiple regression models. A number of previous studies have concentrated on the eastern (Panitsa et al. 2006, 2010) and southern (Kagiampaki et al. 2011) areas of the Aegean archipelago, and the present study therefore differs in a number of respects by focusing on an overlooked area of the archipelago, the Cyclades. It is based on a larger, updated and more detailed database than previous studies (Kallimanis et al. 2010, 2011), as we now have access to newly recorded data (e.g. Kougioumoutzis et al. 2012b), together with the bibliographical resources available for the Cyclades.

In the context of the increasing global biodiversity loss, identifying the factors which affect native plant assemblages is becoming ever more important. Of greatest importance are the endemics, the most valuable botanical resource. Although numerous studies have focused on the factors governing plant species richness, relatively little attention has been given to the drivers of endemic species richness. It is therefore important to understand the factors which influence the diversity of endemic taxa and how these factors affect their distribution. According to Guilhaumon et al. (2008), species–area relationships (SAR) are widely used in establishing the broad patterns of biodiversity that underpin the selection of priority areas for biological conservation.

The aim of the present study was to investigate the effect of a number of environmental factors which shape native and endemic plant species richness in the phytogeographical area of the Cyclades, as well as to pinpoint plant diversity hotspots in the Cycladic islands and the SAVA. We have for the first time tested the role of climate, geological diversity and human disturbance in shaping the assembly of plant taxa in the Cyclades, a rather overlooked part of the Aegean archipelago, and we have compared the results of our analysis with those of other studies covering adjacent phytogeographical areas (Panitsa et al. 2006, 2010; Kallimanis et al. 2010, 2011; Kagiampaki et al. 2011). In particular, we have addressed the following questions:

- How does richness vary as a function of area and elevation in the phytogeographical area of the Cyclades?
- Do other factors, such as geodiversity, climate and human disturbance, affect plant taxon richness?
- Do the environmental factors examined affect plant diversity in different ways in the various areas of the Aegean archipelago?
- Are the Cyclades indeed floristically impoverished, or are there some islands that can be regarded as plant diversity hotspots?

Materials and methods

Dataset 1

The vascular plant species and subspecies of 16 Cycladic islands, mainly of continental origin, except those belonging to the SAVA (namely, Milos, Kimolos, Polyaegos, Santorini and Anafi), all with a relatively well-known flora, were included in the present study and were grouped as Dataset 1 (Figure 1, Table 1). The islands for which detailed floristic data were available included Andros (Snogerup et al. 2006), Anafi (Kougioumoutzis et al.

Table 1. Plant species richness and values of the explanatory variables used for the Cycladic islands included in the present study (Dataset 1). Abbreviations of island names are as in Figure 1. A is area (km^2); E the maximum elevation (m); R the mean annual precipitation (hm^3); G the number of geological substrates; D_m the shortest distance from the nearest mainland (km); and HD the human population density (people/km^2). Abbreviations are as in Figure 1. S_{Nat}, S_F, S_S, $S_{T\text{-}End}$, S_{Cyc} and S_{SA} are the number of total native, fern, spermatophyte, Greek endemic, Cycladian endemic and South Aegean endemic taxa, respectively.

Island	A	E	R	G	D_m	HD	Total	S_{Nat}	S_F	S_S	$S_{T\text{-}End}$	S_{Cyc}	S_{SA}
Am	121	823	45.9	5	117.8	15.35	539	536	5	531	41	11	5
An	38	584	14.4	8	207.1	5.95	635	618	5	613	37	4	7
And	380	1003	132.6	6	55.6	24.13	1065	1015	22	993	46	5	0
Antp	35	301	13.3	5	112.2	26.34	426	418	2	416	17	2	0
Fol	32	415	12.1	3	130.8	24.21	359	358	3	355	28	4	4
Gi	17	490	27.7	1	38.9	0.00	239	238	0	238	6	1	0
Kim	36	364	13.6	3	100.1	17.28	290	289	0	289	15	2	3
Kyt	99	336	34.5	2	37.3	13.08	502	495	2	493	28	4	2
Mi	151	748	57.2	5	103.1	30.97	915	884	10	874	48	5	3
Na	428	999	162.2	7	130.1	39.20	1069	1038	18	1020	53	13	2
Pa	194	724	73.9	8	114.5	69.84	843	821	10	811	35	8	0
Pol	18	350	13.6	2	108.4	0.00	271	270	3	267	10	2	0
Sant	76	567	28.8	3	177	168.28	589	560	13	547	20	3	2
Ser	74	585	27.7	6	62.5	19.68	723	703	11	692	30	5	0
Sik	41	600	15.5	3	142.4	6.12	392	388	5	382	25	4	3
Syr	84	442	31.8	6	58.5	209.91	632	614	9	605	17	1	0

2012b), Antiparos and Paros (Raus 1986), Giaros (Tzanoudakis 1981), Milos (Raus 2012), Naxos (Böhling 1994), Santorini (Hansen 1971; Raus 1988) and Serifos (Livaniou-Tiniakou et al. 2003). For some of these islands the main bibliographical references have been enriched by additional data published subsequently (see supplementary Table S1). For the other islands, data on total and endemic taxa were obtained from Rechinger (1943), Snogerup (1994), Phitos et al. (1995, 2009), Runemark (1996, 2000, 2006), Strid and Tan (1997, 2002), Tan and Iatrou (2001), Thanopoulos (2007), as well as data extracted from the database of the Global Biodiversity Information Facility (GBIF) (2012). The complete list of bibliographical references used to compile the species lists for the islands are given in supplementary Table S1. Dataset 1 includes both species and subspecies. Islands with incomplete floristic data were excluded (e.g. Tinos, Sifnos, Kea and Mykonos) from the analysis; their exclusion reduced the noise and did not affect the trends presented in this study. We also excluded naturalised and alien floras (Arianoutsou et al. 2010). Species nomenclature follows Tutin et al. (1964–1980, 1993), Davis (1965–1985), Pignatti (1982), Tan and Iatrou (2001), Greuter et al. (1984–1989), Greuter and Raab-Straube (2008) and Strid and Tan (1997, 2002). The nomenclature of the endemic taxa is based on Tan and Iatrou (2001) and Georghiou and Delipetrou (2010).

The native taxa (S_{Nat}) were divided into two categories: ferns (S_F) and spermatophytes (S_S).

The endemicity of plants was estimated at different levels (Panitsa et al. 2010), as follows:

- The total number of endemics ($S_{T\text{-}End}$) of a single island is the sum of the taxa that had a distribution range restricted to Greece,
- Cycladian endemics (S_{Cyc}) are taxa with a distribution range limited to the Cyclades (Strid and Tan 1997), and
- South Aegean endemic taxa (S_{SA}) are taxa with a distribution range limited to the phytogeographical regions of Kriti–Karpathos and the Cyclades (Strid and Tan 1997).
- We did not include single island endemics in our analysis, since the vast majority of the Cycladic islands do not host such taxa (the exceptions being Amorgos, Andros and Naxos). The numbers of S_{Nat}, S_F, S_S, $S_{T\text{-}End}$, S_{Cyc} and S_{SA} which constitute the response variables, as well as the geographical, climatic, geological and topological data for Dataset 1 are given in Table 1.

Dataset 2

Additional data were obtained for 30 additional Aegean islands and peninsulas to allow us to determine the relative importance of the plant diversity hotspots of Dataset 1 within the context of the whole south Aegean Sea. These islands, which together with Dataset 1 comprise Dataset 2 (supplementary Figure S1), include 21 East Aegean Islands (Panitsa et al. 2010), seven South Aegean Islands (Kagiampaki et al. 2011), as well as Aegina Island (Vallianatou 2005) and the Methana peninsula (Kougioumoutzis et al. 2012a) from the Saronic Gulf. Data regarding Nisyros was derived from Papatsou (1974), Burton (1991), Strid and Tan (1997, 2002), Tan and Iatrou (2001) and Thanopoulos (2007), and the GBIF database (2012).

Analysis

To explore the effect of key biological, geographical and climatic variables on the species richness of Dataset 1, the determinants of the six species richness metrics (S_{Nat}, S_F, S_S, $S_{T\text{-}End}$, S_{Cyc} and S_{SA}) were modelled by two complementary approaches: (1) the island species–area relationships (ISARs) and (2) multiple regression analysis. These explanatory variables were:

- Area (A, km^2), which is the most powerful single explanatory variable of species richness (MacArthur and Wilson 1967; Rosenzweig 1995; Whittaker and Fernández-Palacios 2007).
- Maximum elevation (E, m), which is used as a surrogate of habitat heterogeneity, as the latter is complex, multifaceted and difficult to quantify from the perspective of the target organism in an objective and repeatable fashion (Triantis et al. 2008).
- Shortest distance from the nearest mainland (D_m, km), which together with area have emerged as the strongest drivers of island species richness at global (Kreft et al. 2008) and regional scales (Cody 2006).
- Annual precipitation (R, hm^3), which can be used as a good climatic predictor of species richness (Francis and Currie 2003).
- Number of geological substrates (G), as ecological and historical processes might be strongly influenced by geology (Mueller-Dombois 2002; Whittaker and Fernández-Palacios 2007), and this variable has been shown to be a strong determinant of species richness on the global scale (Kreft et al. 2008).
- Human population density (HD, people/km^2), which is a good proxy for several human-mediated processes (Pautasso 2007). Moreover, high human population density is often related to low biodiversity (Pärtel et al. 2007).

A, E and D_m were determined from 1:50,000-scale digital topographic maps obtained from the Hellenic Military Geographical Service (web.gys.gr/GeoSearch/). The geological information (G) was compiled from the 1:500,000-scale geological map of Greece (Bornovas and Rondogianni-Tsiambaou 1983), while data regarding R were determined according to Koutsogiannis et al. (2008). Data regarding HD was extracted from the Hellenic Statistical Authority report (2011). We did not include a variable directly describing habitat heterogeneity as other studies have done for adjacent phytogeographical regions (Panitsa et al. 2006, 2010; Kallimanis et al. 2010, 2011; Kagiampaki et al. 2011), since the number of vascular plant species richness on a given island is highly predictable from a few relatively simple island characteristics (Kreft et al. 2008). Moreover, Ibáñez and Effland (2011) state that soil-forming factor diversity (physiographic, climate and litho-diversity) is equivalent to habitat diversity. Furthermore, while habitat heterogeneity is already included in ecological theory as a vague term (Whittaker et al. 2008), it is neither precisely defined nor measured in a standardised manner (Steinbauer et al. 2013). Finally, as Kallimanis et al. (2008) state, the dominant effect of habitat diversity on the species–area relationships (SARs) is to increase the slope of the SARs.

ISARs were investigated for Dataset 1 by fitting the logarithmic transformation of the Arrhenius (1921) power model (described hereafter as the power function model):

$$\log(S) = c + z^{*}\log(A), \tag{1}$$

where S is the value of each of the richness metrics used, A is the area of the respective island in km^2 and c and z are the fitted parameters. Since zero values were reported for some islands, a value of 1 was added to S_F and S_{SA} before $\log_{10}$ transformation. We compared the models using R^2 values as a measure of their goodness of fit. Since the models have the same number of fitted parameters, the R^2 values are directly comparable without any modification (Triantis et al. 2003, 2005). The z parameter was used for preliminary comparison between the floristic diversity of the Cyclades and other Aegean islands.

Most of the variables had frequency distributions that were strongly positively skewed. The variables were therefore transformed to normalise their distribution so that they could be compared with bivariate and multivariate regression methods without heteroscedastic biases, and to improve the linearity of the relationships in the regression models. Since all variables consisted of count data, they were normalised by logarithmic (base 10) transformation. A goodness of fit test (Shapiro–Wilk and Kolmogorov–Smirnov, with 95% level of confidence) to a normal distribution was used to confirm that each transformed variable had been successfully transformed to an approximately normal distribution.

To investigate the combined effects of the six biogeographical factors (A, E, D_m, R, G and HD) on the six species richness metrics (S_{Nat}, S_F, S_S, $S_{T\text{-}End}$, S_{Cyc} and S_{SA}) of Dataset 1, we applied stepwise multiple regressions, using a different species richness metric as a response variable each time. This process also allowed the calculation of partial coefficients of determination (r^2) for each explanatory variable, which captured the percentage of variation explained by each factor when the other factors were held constant. In order to avoid the inclusion of collinear explanatory variables, only factors with a tolerance value larger than 0.05 and total condition index <100 were retained. All regressions and the estimations of the parameters were carried out in IBM SPSS 19.

By fitting this full model, the total adjusted coefficient of multiple determination (R^2_{adj}) was assessed.

Spearmann's correlation coefficient was used for all pair-wise correlations among all species richness metrics.

Finally, in order to compare the floristic diversity between islands of different size and to locate possible Cycladic plant diversity hotspots, we used the values of the residuals from the ISAR $\log_{10}$-transfomed models of S_{Nat}, $S_{T\text{-}End}$ and S_{Cyc}, as these values may be interpreted as a measure of island species diversity and are not influenced by island area (Hobohm's α-index; Hobohm 2000, 2003). Positive and negative values of the Hobohm's α-index refer to areas with species diversity above and below average, respectively (Hobohm 2000, 2003). Subsequently, in order to establish their relative importance as plant diversity hotspots in the south Aegean Sea, we ran two separate ISAR $\log_{10}$-transfomed models for S_{Nat} and $S_{T\text{-}End}$ for Dataset 2.

Results

Species richness

The total number of taxa occurring in Dataset 1 was 1835, increasing the number of taxa known to occur in the Cyclades by 195. Only 25 of the taxa were endemic to the Cyclades. Among all recorded taxa, 179 were found on more than nine of the islands and 21 taxa were distributed on all the islands studied. The number of native taxa per island varied from 238 to 1038 (Table 1). The proportion of Greek endemics and Cycladian endemics to the total native taxa ranged from 2.5 to 7.8% and 0.4 to 2.1%, respectively, whereas the proportion of Cycladian endemics to Greek endemics ranged from 5.9 to 26.8%.

Species–area relationships

The ISAR power function model explained a higher proportion of variance for S_S than for S_F or S_{Nat} (supplementary Table S2). The z parameters of the ISAR power function models demonstrated a sequential increase from S_{Nat} to S_{Cyc} (supplementary Table S2). The c and z values were much smaller for S_F and S_{Cyc} than for the rest of the metrics, reflecting the fact that ferns and Cycladian endemics are almost absent from smaller islands. However S_F increased with increasing area more steeply than the richness of any other category.

Predictors of species richness

Separate simple linear regressions of all the species richness metrics were applied in order to compare the performance of the explanatory variables (supplementary Table S2). The analysis of Dataset 1 confirmed A as the most powerful single explanatory variable of island species richness, while G, E and R also explained a large

Table 2. Summary statistics for predictive models of S_{Nat}, S_F, S_S, $S_{T\text{-}End}$, S_{Cyc} and S_{SA} with *A*, D_m, *E*, *G*, *HD* and *R* for Dataset 1. All variables are $\log_{10}$-transformed. For each significant predictor included in the minimal model after stepwise variable selection, the following results are reported: the explained variance expressed using the coefficient of determination R^2, the sign of the estimated relationship between the response and the predictor, the partial coefficients of determination r^2 and the tolerance value of each predictor. Total variance explained by each model was calculated using the R^2-adjusted statistics. Abbreviations are as given in Table 1.

	Coefficient	Beta	R^2_{Cum}	R^2_{adj}	r^2	F	*P*	Tolerance
S_{Nat}								
c		1.95						
A	+	0.32	0.83	0.82	0.87	68.85	<0.001	0.60
G	+	0.30	0.92	0.90	0.71	70.88	<0.001	0.60
S_S								
c		1.95						
A	+	0.32	0.83	0.82	0.87	68.95	<0.001	0.60
G	+	0.30	0.92	0.90	0.71	71.68	<0.001	0.60
S_F								
c		−0.59						
A	+	0.74	0.59	0.56		20.21	0.001	
$S_{T\text{-}End}$								
c		−0.92						
A	+	1.29	0.64	0.61	0.90	24.62	<0.001	0.08
R	–	−1.14	0.79	0.76	−0.87	24.40	<0.001	0.11
E	+	0.64	0.88	0.85	0.63	28.78	<0.001	0.33
HD	–	−0.12	0.92	0.89	−0.56	30.19	<0.001	0.42
S_{Cyc}								
c		−3.16						
E	+	1.31	0.49	0.45		13.48	0.003	
S_{SA}								
c		−0.76						
D_m	+	0.58	0.29	0.24		5.68	0.03	

proportion of the variance for almost all the species richness metrics (supplementary Table S2); *G* explained a large proportion of variance for S_{Nat} (R^2 = 0.62). In the case of S_{SA}, only D_m emerged as a significant explanatory variable, but had relatively weak predictive power (supplementary Table S2).

Predictive modelling

A and *G* were retained in the optimal model for S_{Nat} and S_S, while *A* together with *E*, *R* and *HD* were retained in the optimal model for $S_{T\text{-}End}$ (Table 2). *E* could be used as a predictor of S_{Cyc}, while D_m was the only factor that entered the model for S_{SA} and *A* was the only factor entering the model for S_F (Table 2).

Locating plant diversity hot-spots

Using the α-index (Table 3), Anafi and Serifos presented values well above average (2.235 and 1.424, respectively), whereas Kimolos gave the lowest value (–1.496). Four islands could be regarded as floristically impoverished (very low α-values), namely Giaros, Kythnos, Amorgos and Kimolos. For the endemic elements Anafi and Folegandros obtained remarkably high values (1.920 and 1.402, respectively), while Giaros gave the lowest value (–1.882). Anafi, Milos and Serifos had high α-values for both total native and Greek endemics (Figure 2), while Andros, Naxos, Kimolos and Polyaegos displayed low α-values for both species richness metrics. Amorgos, along with Anafi and Folegandros, were islands with high α-values for both total native and Cycladian endemics (Figure 3), while Andros, Giaros and Syros gave low α-values for both species richness metrics.

In the case of Dataset 2, Anafi had the highest α-value for both total native and Greek endemic taxa (Figure 4), along with a group of islands, mainly of volcanic origin apart from Serifos, which demonstrated high values for both species richness metrics; Oinousses displayed the

Table 3. Values of the α-index for the total native taxa (S_{Nat}), the Greek endemic taxa ($S_{T\text{-}End}$) and the Cycladian endemic taxa (S_{Cyc}) for Dataset 1.

Island	Alpha-S_{Nat}	Alpha-$S_{T\text{-}End}$	Alpha-S_{Cyc}
Amorgos	−1.030	0.673	1.518
Anafi	2.235	1.920	0.796
Andros	−0.311	−0.524	−1.019
Antiparos	0.436	−0.049	−0.384
Folegandros	−0.152	1.402	0.962
Giaros	−0.830	−1.882	−0.948
Kimolos	−1.496	−0.420	−0.412
Kythnos	−0.993	−0.082	−0.127
Milos	1.017	0.803	−0.129
Naxos	−0.458	−0.302	0.603
Paros	0.092	−0.370	0.484
Polyaegos	−0.317	−0.592	0.257
Santorini	0.213	−0.634	−0.395
Serifos	1.424	0.484	0.559
Sikinos	−0.289	0.773	0.723
Syros	0.460	−1.199	−2.489

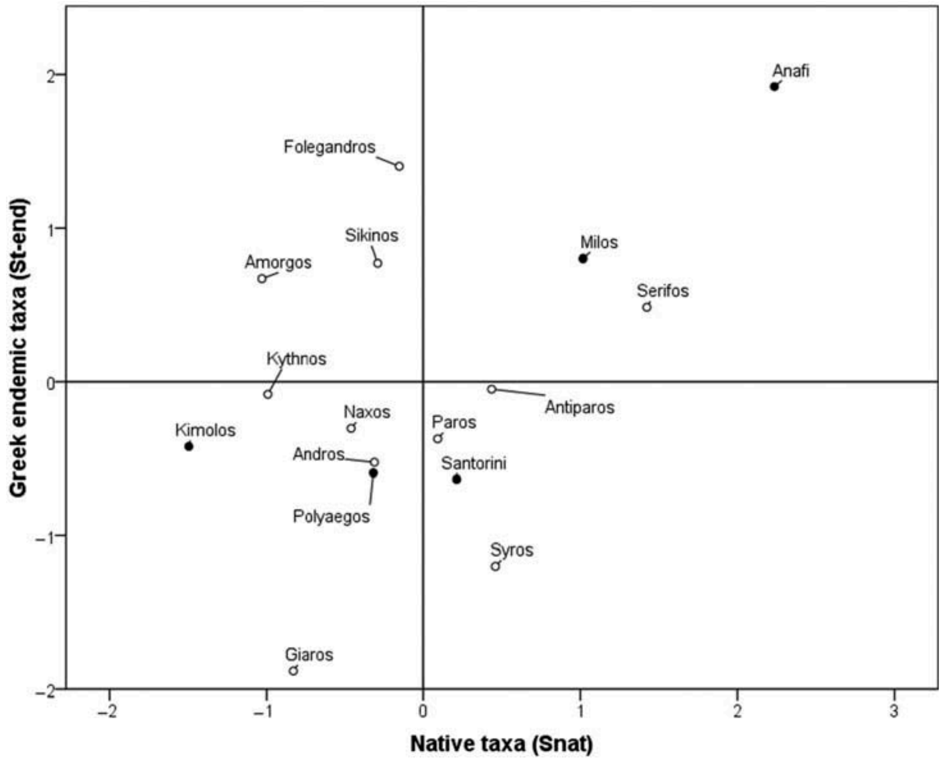

Figure 2. Plot of residuals of Greek endemic taxa ($S_{T\text{-}End}$, y-axis) versus native taxa (S_{Nat}, x-axis), as estimated from the ISAR power function model for Dataset 1. Black circles indicate the members of the SAVA included in the present study. Abbreviations as in Table 1.

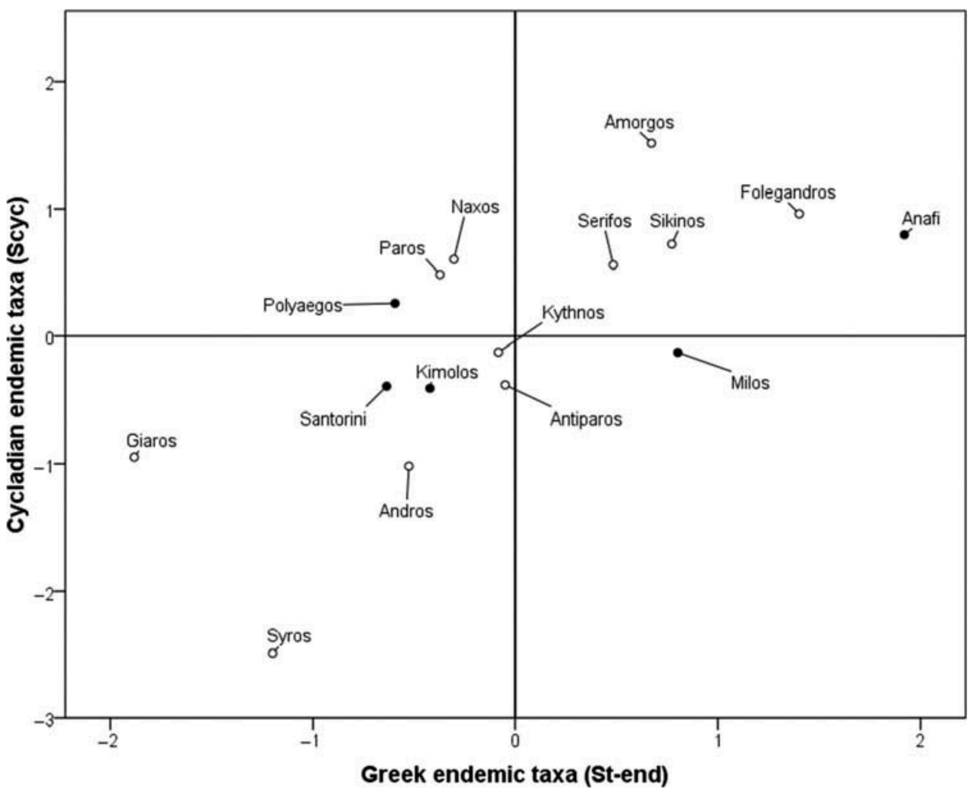

Figure 3. Plot of residuals of Cycladian endemic taxa (S_{Cyc}, y-axis) versus Greek endemic taxa ($S_{T\text{-}End}$, x-axis), as estimated from the ISAR power function model for Dataset 1. Black circles indicate the members of the SAVA included in the present study. Abbreviations as in Table 1.

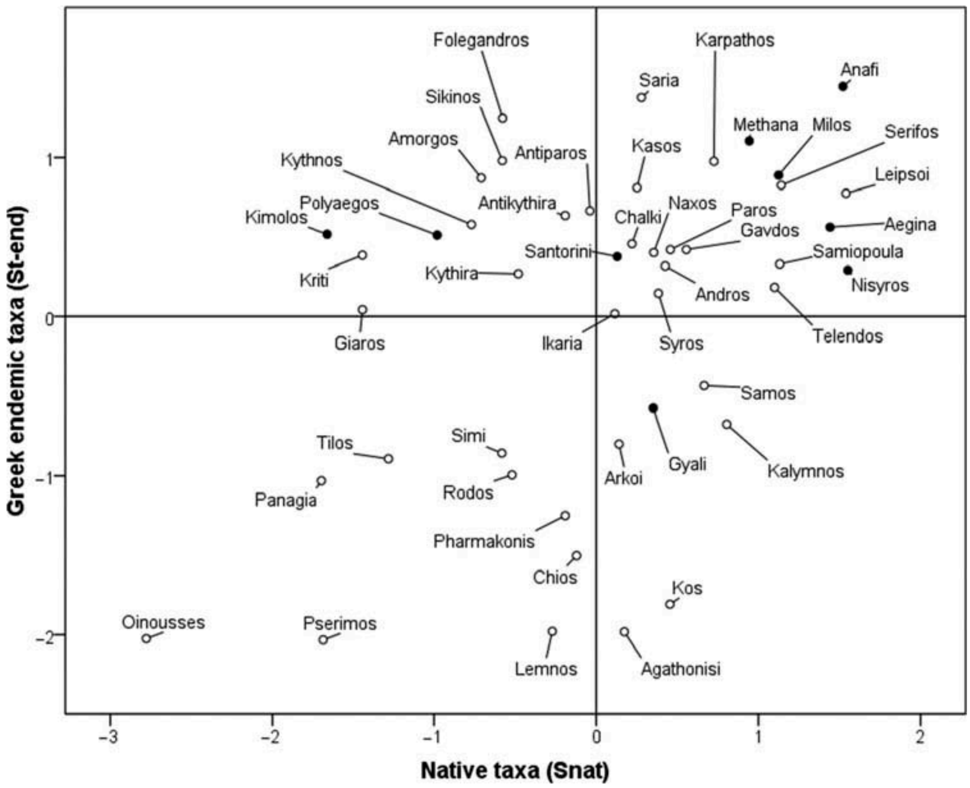

Figure 4. Plot of residuals of Greek endemic taxa ($S_{T\text{-}End}$, y-axis) versus native taxa (S_{Nat}, x-axis), as estimated from the ISAR model for Dataset 2. Black circles indicate the members of the SAVA included in the present study. Abbreviations as in Table 1.

lowest α-values for both species richness metrics. The α-values for S_{Nat} and $S_{T\text{-}End}$ of Dataset 2 are shown in supplementary Table S3.

Discussion

Species–area relationships

The analysis of Dataset 1 confirmed that was in general area the most powerful single explanatory variable of island species richness (Rosenzweig 1995; Whittaker and Fernández-Palacios 2007) and in the Aegean (Panitsa et al. 2006; Kallimanis et al. 2010; Kagiampaki et al. 2011). Our power function model had an overall predictive capacity of $R^2 = 0.82$ and is in line with the results of Kreft et al. (2008), who reported $R^2 = 0.66$ for the ISAR fitted by the Arrhenius model on the total flora of 488 islands across the globe. It is also in line with the R^2 value reported for the East Aegean archipelago (0.893, Panitsa et al. 2010), the South Aegean island arc (SAIA; 0.85, Kagiampaki et al. 2011) and for some Aegean islands (0.947, Trigas et al. 2008). The z parameter of the power function model ($z = 0.43$) was larger than those found in SAIA (0.39, Kagiampaki et al. 2011), the East Aegean archipelago (0.326, Panitsa et al. 2010) or for some Aegean islands (0.281, Trigas et al. 2008), while it was similar to that of 86 East Aegean islets (0.40, Panitsa et al. 2006). In our case, the ISAR z value was consistent with the higher floristic heterogeneity values observed in isolated floras, as it fell within the range 0.2–0.5, proposed by Rosenzweig (1995) for island groups or isolated habitat patches. It therefore seems that the Cyclades are characterised by a more isolated flora than the East Aegean islands or the islands comprising the SAIA. One reason why the Cyclades seem to have an isolated flora is that we included in our analysis a number of volcanic Aegean islands, which by nature are more isolated than land-bridge islands. Additionally, our estimated slope is almost identical to that found for volcanic islands around the globe (Kreft et al. 2008).

Predictors of species richness

Precipitation (R). Kreft et al. (2008) stated that precipitation had an insignificant or weak effect on island species richness. On the other hand our results indicate that R has a strongly negative impact on $S_{T\text{-}End}$; the wetter the conditions, the fewer the endemic Greek taxa present on a given Cycladic island. This is not surprising, as many of the Greek endemic taxa are adapted to a water-deficient environment and prefer habitats with high stress level, where competition is low (Panitsa et al. 2010). High stress level habitats in the Mediterranean area are mainly correlated with the abundance of endemics, as indicated by the dominance of stress tolerators in the endemic flora and the habitat types they occupy (Médail and Verlaque 1997; Trigas et al. 2008). Moreover, contemporary climate may constrain the number of individuals, and hence the number of species, or may alternatively limit the number of successful colonisers from nearby continents (Kreft et al. 2008). This could mean, at least for the Cyclades, that mean annual precipitation could be considered to be the main explanatory factor for the low number of species (whether endemic or not) occurring in the Cyclades compared with surrounding phytogeographical areas. From this perspective, *R* seems to have a constraining dispersal effect on widespread Greek endemic taxa in the Cyclades. Since the East Aegean islands and the Peloponnese have a significantly wetter climate than the Cyclades, it is highly likely that the majority of the Greek endemics occurring there do not prefer the water-deficient environments that prevail in most of the Cyclades; this is most likely the reason why several East Aegean and Peloponnesian endemics are absent from the Cyclades. These findings provide support to the term “Kykladenfenster” (Cycladic window) coined by Rechinger (1950) to describe the absence from the Cyclades of certain taxa that are present in the surrounding continents.

Variety in geological substrates (G). Geology has emerged as a strong predictor in an analysis of 488 islands across the globe (Kreft et al. 2008). In our analysis the effect of *G* on total plant species richness was significant, concurring with the results of Kreft et al. (2008), and also in accordance with Hjort et al. (2012), who stated that consideration of explicit measures of geodiversity can improve species richness models in a fundamental manner at mesoscale resolution. Our results also provide support for the findings of Kallimanis et al. (2010), who assumed that there might be a positive correlation between total species richness and the richness of geological substrata in the Aegean archipelago. It appears that, at least for the Cyclades, geologically more diverse islands offer a variety of different and available ecological niches, which in turn may be the reason for the higher than average plant diversity on some Cycladic islands (e.g. Anafi). This is in accordance with Ibáñez and Effland (2011) who stated that pedodiversity is a reasonable surrogate indicator of biodiversity and that the main driving force of pedodiversity is plate tectonic dynamics. The latter is probably the reason why Anafi and the islands comprising SAVA, which were created as the result of plate tectonic dynamics, demonstrate exceptionally high plant species richness.

Human population density (HD). HD appears to have a negative effect on $S_{T\text{-}End}$. The negative effect of *HD* on $S_{T\text{-}End}$ possibly reflects the effect of the continuous, uninterrupted and strongly growing human presence over about eight millennia, which according to Blondel (2008) has resulted in dramatic changes to the composition and structure of those landscapes in the Mediterranean islands which are less resistant and resilient than mainland areas. Collins et al. (2012) have also attributed the changes in the composition and structure of landscapes in the Mediterranean islands to anthropogenic activity, as well as to the climate changes that occurred during the late Holocene. According to Greuter (1979, 1995, 2001), nearly 45% of the present Aegean flora reached the Aegean islands as the result of human action in prehistoric or early historic times; a large part of the Aegean flora is synanthropic (occurring in man-made habitats or in habitats affected by livestock) and the proportion of such species in the Aegean increases with grazing (Bergmeier and Dimopoulos 2003). Greuter (1995) also noted that these synanthropic species may be perfectly integrated into native plant communities. On the Cyclades, the present endemic flora occurs almost exclusively in habitats that are inaccessible to man and his domestic animals (Snogerup 1985). According to Runemark this phenomenon (1971) may be attributed to the less competitive nature of the endemic Aegean flora to this kind of pressure; most endemic species do not belong to a climax community and do not grow in the habitat which is most suitable for them, but only in habitats where stronger competitors allow them to grow (Runemark 1971). Panitsa and Tzanoudakis (2001) speculated that losses of endemic species in the eastern Aegean were presumably induced by human overexploitation, while according to Cellinese et al. (2009) island endemics in the Aegean area may have been more widespread in the past, but are now often restricted to inaccessible areas, probably as a result of human pressure. Evidence thus suggests that human influence has played a major role in shaping the pattern observed in the endemic species present in the Cyclades. Finally, in areas where human population and disturbance continue at a very high level (i.e. in the Cycladic islands), there will eventually be a decline in total plant species richness (Kornas 1983; Kowarik 1995; McKinney 2002). This is evident in many Aegean islands, as a few non-native weeds and aliens cover immense areas (Arianoutsou et al. 2010; Kougioumoutzis et al. 2012b).

Elevation (E). Our results indicate that *E* plays an important role in shaping plant diversity patterns in the endemic categories, and they concur with previous studies in other parts of the Aegean archipelago (Kallimanis et al. 2010, 2011; Panitsa et al. 2010; Kagiampaki et al. 2011), according to which maximum elevation is a major contributor to the prediction of endemic species richness. However, elevation does not seem to be the most important variable related to endemic species richness, at least in the Cyclades, in contrast to the findings of Kallimanis et al. (2010) regarding the Aegean archipelago. On local scales, *E* can still predict Cycladian endemics, a finding agreeing with that of Panitsa et al. (2010) for Aegean and single island endemics in the East Aegean islands. This result is in accordance with Rechinger (1965), who stated that Aegean endemics are mainly ancient mountain endemics with distribution areas older than the current land/sea distribution, since the present-day Aegean islands were mountain-tops in the geological past. Indeed, the Aegean limestone cliffs very often harbour endemic taxa (Tzanoudakis et al. 2006). As Snogerup states (1995), the Kalamos Peninsula in Anafi is one of the most important cliff refugia in the Aegean, as more than one-third (37.8%) of the endemic flora of Anafi is located there (Kougioumoutzis et al. 2012b) at elevations below 500 m a.s.l., and it includes a number of rare endemic taxa such as *Campanula laciniata*, *Sedum littoreum* var. *creticum* and *Sternbergia greuteriana*. This phenomenon can be also observed in many other Cycladic islands, such as Amorgos (Snogerup 1995) and Naxos, where the central mountain areas host local or very restricted endemics (Phitos et al. 1995; Strid and Tan 1997; Phitos et al. 2009). There appears to be a rise in Greek endemic species from sea level to 600 m a.s.l, followed by a steep fall at altitudes above this in the Greek islands; this phenomenon is attributed to the lack of high altitudes on most Aegean islands (Georghiou and Delipetrou 2010). In the Cycladic islands, on the other hand, at elevations >600 m a.s.l. an increase in mean annual precipitation appears to be inversely related to endemic species richness.

Shortest distance from the nearest mainland (Dm). Distance appears to play a minor role in shaping plant diversity patterns in the Cyclades and it explains the small proportion of variance in the South Aegean endemics. This possibly indicates that the islands comprising the SAVA, as well as the rest of the Cyclades, are detached from their neighbouring continents (Sterea Ellas, Peloponnese and Asia Minor) in terms of phytogeography, whereas the opposite is true for the East Aegean (Panitsa et al. 2010) and South Aegean archipelago (Kagiampaki et al. 2011). This is not surprising, bearing in mind the complex palaeogeographical history of the Cyclades and the fact that several eastern and southern Aegean Islands were connected to the nearest mainland until the Pleistocene period (Sondaar 1971; Dermitzakis 1990).

Habitat diversity

Although the a variable incorporating the effects of habitat diversity on species richness was not included in the analysis, the different Cycladic plant species richness metrics are relatively well approximated compared to other studies in the Aegean area which include this variable. This concurs with Kreft et al. (2008), who stated that the number of vascular plant species richness on a given island is highly predictable from a few relatively simple island characteristics. More specifically, the stepwise multiple regression analysis had an overall predictive capacity of R^2 = 0.90, while Panitsa et al. (2010) report R^2 = 0.952 for the East Aegean Islands and Kagiampaki et al. (2011) reported R^2 = 0.87 for SAIA. Our results seem to be in accordance with Kallimanis et al. (2008), who stated that the dominant effect of habitat diversity on the species-area relationships (SARs) is to increase the slope of the SAR.

Plant diversity hot-spots

Dataset 1. Our results indicate that Anafi and Serifos in fact constitute plant diversity hotspots, while islands with a large number of total native and Greek endemic taxa, like Andros or Naxos are not characterised as such. The identification of biodiversity hotspots has traditionally focused either on the total number of species or on the numbers of endemic or threatened species (Smith and Theberge 1986; Myers et al. 2000). Diversity and the presence of rare species are the most frequently cited criteria for site selection by conservationists (Margules and Usher 1981; Usher 1986; Scott et al. 1993). However, endemic or threatened species can be misleading in the prediction of total species diversity when evaluating areas and identifying ecological hotspots (Prendergast et al. 1993; Andelman and Fagan 2000; Bonn et al. 2002), and should be used with caution. For instance, within the Cyclades there are islands thought to have a low proportion of endemism, such as Serifos, and others such as the dry south-eastern islands (mainly Anafi and Astypalaea), which have in the past been considered floristically unimportant. Geologically more diverse islands in the Cycladic archipelago, such as Anafi and Serifos, contain proportionally more Greek and Cycladian endemic taxa than geologically less diverse islands, possibly due to the numerous ecological niches available. Moreover, the geographical position and the palaeogeographical history of a given island could be equally important in shaping Cycladic plant species diversity; as more migration routes intersect, the greater the number of taxa on the island. This is apparent in the case of Anafi, in which at least two migration routes, of south- and eastward origin, intersect (Kougioumoutzis et al. 2012b).

Dataset 2. The phytogeographical region of the Cyclades has long been considered to be floristically impoverished by comparison with other island regions of Greece (Phitos et al. 1995). Our comparative analysis of 46 Aegean islands (Dataset 2) indicates that although the islands comprising the phytogeographical area of the Cyclades are indeed as a whole floristically impoverished, two islands, Anafi and Serifos, are plant diversity hotspots in the South Aegean context, having higher α-index values than islands long regarded as the most important centres of Greek plant diversity, such as Kriti or Karpathos. However, Kriti and Karpathos still remain a hotspot for endemic taxa, and actually, Kriti is confirmed as a speciation hotspot in the Mediterranean region (Trigas et al. 2013 and references therein). Furthermore, the vast majority of the SAVA, together with Andros, Paros and Antiparos, have higher α-values than Ikaria and Rodos, two islands considered highly important in terms of phytogeography and endemism (Carlström 1987; Christodoulakis 1996).

Conservation strategies

The SAVA appears to be of considerable conservation value, as many areas within it host native and Greek endemic taxa well above average. In addition, $S_{T\text{-}End}$ and S_{Cyc} show a strong positive association with S_{Nat} and with one another (0.821, 0.716 and 0.818, respectively), in contrast to previous studies that have reported low association between overall species diversity and endemic species richness for Greek endemic plants (Dimitrakopoulos et al. 2004; Trigas et al. 2007; Panitsa et al. 2010). This disagreement may be attributed to the different response of the endemic categories and S_{Nat}, since *A*, *E*, *R* and *HD* explain $S_{T\text{-}End}$, *E* explains S_{Cyc}, while *A* and *G* explain S_{Nat}. Different conservation strategies should therefore be developed for total and endemic species diversity in the Cycladic islands. Furthermore, the high correlation between $S_{T\text{-}End}$ and S_{Cyc} implies that conservation strategies focusing on total endemic diversity would probably also be appropriate for Cycladian endemic taxa. Geodiversity could be used as the focal site selection criterion for conservation planning in the Cyclades; by protecting sites of high geodiversity there is a high probability of also protecting sites harbouring high biodiversity. In addition, it is of the utmost importance to restrict the expansion of alien taxa in those Cycladic islands recognised as plant diversity hotspots; many Aegean islands have suffered by the introduction of alien and invasive taxa, which now occupy large areas (Arianoutsou et al. 2010). Some native plant diversity hotspots may be particularly vulnerable to invasion by exotic plant species (Stohlgren et al. 1999) which may place some native species at a disadvantage (Stohlgren et al. 2001; Arianoutsou et al. 2010).

Conclusions

Area and geology are confirmed as two of the strongest predictors of overall native plant species richness on islands, but it seems that regarding the more narrowly distributed taxa, such as the Greek endemic taxa or taxa only present in the Cyclades, other factors play a role in shaping the plant assembly in the Cyclades. Mean annual precipitation and human population density, two factors not previously considered in the Aegean area, emerge as significant predictors of the Greek endemic taxa present in the Cyclades, while maximum elevation is found to be the only predictor of those taxa restricted to the Cyclades. Human population density was found to have a negative impact on the diversity of Greek endemics, and mean annual precipitation appears to be related to the distribution of several taxa in southern insular Greece (Rechinger 1950). Nevertheless, in a complex system such as the Cyclades, which have a very tangled palaeogeographical history and host a number of phylogenetic lineages, other than the most commonly applied factors influencing plant species richness may have to be embodied in a model trying to explain the plant diversity of the Cycladic islands. Such factors could include the palaeoclimate, the age of the island, the number of times sea level has risen or dropped since the Quaternary on a given island, and the degree of palaeogeographical isolation. This would allow a better understanding of the drivers of the narrow endemics richness, once adequate and reliable data for these factors become available.

Anafi emerges as the most important plant diversity hotspot, not only in the Cycladic archipelago, but also in the whole South Aegean Sea. Moreover, SAVA seems to be not only one of the most significant geological structures in the Mediterranean area, but it also has great conservation value, since the areas it comprises host well above average native and endemic taxa. This suggests that when trying to identify a site that is in need of protection, botanists and other decision makers and conservationists must pay attention to factors other than the sheer number of endemic, rare and threatened taxa on any given island in the Aegean archipelago.

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Supplemental data

Supplemental data for this article can be accessed here.

Notes on contributors

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