Factors affecting plant species richness and endemism in the South Aegean (Greece)

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INTRODUCTION

The South Aegean island arc is ideal for the investigation of species richness patterns. We applied the species-area relationship for overall vascular flora and for endemic plants, as well as for different families, using available floristic data from 60 of its islands. Maximum altitude, shortest distance from mainland and from the nearest larger island, and habitat diversity were examined as potential predictors of species richness. Habitat diversity estimation was based on species light, temperature, moisture and soil salinity requirements, according to the Southern Aegean Indicator Values. The effectiveness of Choros model was also tested. Habitat diversity alone was more effective than area in determining the vascular flora of the 60 islands and of two endemic species categories. The Choros model was the most efficient one in shaping the number of South Aegean endemics. Area prevailed in the case of single island endemics. Our results indicated that both area and habitat diversity should be examined for a more thorough interpretation of richness patterns. Altitude contributed mostly to the prediction of species richness for total flora and for most subsets of endemics. Species-area relationships at the family level varied significantly in relation to the number of species within each family and the family distributional range within the study area. A strong correlation between intercept values arising from species-area relationships at the family level and total richness of these families in the South Aegean supports an ecological interpretation of the intercept as an indicator of the “capacity” of the studied area.

Key words: Choros model, habitats, plant families, Southern Aegean Indicator Values, species richness.

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(Greuter, 1971; Strid, 1996), and its historical and ecological phytogeography (Rechinger & Rechinger-Moser, 1951; Zohary & Orshan, 1965; Greuter, 1970, 1971; Zaffran, 1990; Bergmeier, 2002; Bergmeier & Dimopoulos, 2003). However, to our knowledge, there is no study investigating the relationship between species richness and island area for vascular plants of the South Aegean, although subsets of its islands have been considered in some studies (see Höner & Greuter, 1988; Höner, 1990; Greuter, 1991; Legakis & Kyriotakis, 1994; Bergmeier & Dimopoulos, 2003; Kallimanis et al., 2010; Panitsa et al., 2010).

There are more than twenty proposed models for describing the Species-Area Relationship (SAR) (Tjørve, 2003, 2009; Dengler, 2009; but see also Williams et al., 2009). Nevertheless, the power model of Arrhenius (1921) \( S = c A^z \), where \( S \) is the number of species, \( A \) is the total area of each island, and \( z, c \) are fitted parameters) is most commonly used (for discussion see Scheiner, 2003; Tjørve, 2003; Fattorini, 2007; Dengler, 2009; Williams et al., 2009). According to Rosenzweig (2003, 2004), the “species-area pattern” is composed of three different SARs, whereby processes operating at different spatial and temporal scales (Shmida & Wilson, 1985; Crawley & Harral, 2001) lead to different \( z \)-values (see also Triantis et al., 2008). The values of \( z \) vary according to the geographic scale of the study area: it is typically 0.55-1.00 among biogeographical provinces, 0.1-0.2 within biogeographical provinces, and 0.25-0.55 for islands or isolated habitat patches (Rosenzweig, 2004). Despite the numerous biogeographic studies, almost nothing has been added to our knowledge of the biological significance and statistical behavior of the parameter \( c \) (see MacArthur & Wilson, 1967; Connor & McCoy, 1979; He & Legendre, 1996; Lyons & Willig, 1999; Lomolino, 2001). The parameter \( c \) has been considered as an indicator of the capacity of the studied area to support individuals and species (MacArthur & Wilson, 1967; Connor & McCoy, 1979; Brown & Lomolino, 1998), but there is still not enough evidence corroborating this view. Sfenthourakis (1996) concluded that the values of slopes and intercepts of the species-area regression lines seem to be statistical artefacts that encompass the effects of several intervening factors, such as the data set size and range. Therefore, they should be checked accordingly before any biological statements about differences between taxa or island groups can be made (Sfenthourakis, 1996).

Increase in area and increase in habitat diversity have long been identified as the two major mechanisms of species addition on islands (for a review, see Whittaker & Fernández-Palacios, 2007). These mechanisms are theoretically supported by the area \textit{per se} and the habitat diversity hypotheses, respectively. Despite the debate on the superiority of one mechanism over the other, a more plausible interpretation is that they are supplementary, not mutually exclusive (see Triantis et al., 2003; Sfenthourakis & Triantis, 2009; Hortal et al., 2009). Simberloff (1988) pointed out that the majority of SARs documented so far is accounted for by the fact that larger sites have more species, not only because the area is larger, but also because larger sites include more habitats than smaller ones; thus, in some cases habitat diversity alone explains species richness better than area.

In order to identify and understand the interplay between heterogeneous mechanisms driving diversity in space and time, a “deconstructive approach” can be quite informative. Species richness is a generalized variable that subsumes in a single number the variety of life found at a particular point in time or space (Marquet et al., 2004). Nevertheless, individual species are not equal or ecologically equivalent. According to Marquet et al. (2004), the deconstructive approach is “the analytical strategy of disaggregating species richness into smaller subsets of species which share a particular characteristic, such as mode of development or other phylogenetic, ecological, or life history trait“, subsequently giving rise to richness patterns (Huston, 1994). Endemics and families constitute subsets of species, which can be used in such a deconstructive approach.

The scope of this work was to study patterns of plant species diversity in the South Aegean island arc. We examined the relationship between vascular plant species and islands area. We also tested the contribution of habitat diversity and various physiographic factors in shaping the SAR. Additionally, we deconstructed the SAR by considering ecologically and evolutionarily defined species groups, i.e. plant families and endemics at various levels of endemism.

**MATERIALS AND METHODS**

**Study area and data set**

The South Aegean islands are mainly of continental origin. They form a land-bridge, connecting the coasts of the southeastern continental part of Greece (Peloponnisos) with southern Asia Minor and forming the
southernmost barrier of the Aegean archipelago (Fig. 1). Crete, Rodos, Karpathos and Kythira are the largest islands, with high mountains, numerous gorges and some permanent surface water. Gavdos is the southernmost island, located ~37 km away from Crete and ~250 km away from the North African Cyrenaica coast. The two sides of the arc, Kythira and Antikythira on the west and Rodos on the east, hold a double floristic position: they are both closely related with the other South Aegean islands, but also exhibit a similarly close relation with their neighboring mainland (Rechinger & Rechinger-Moser, 1951; Carlström, 1986; Strid, 1996). Neolithic settlements, discovered in the study area, dated back to 6100 BC (Rackham & Moody, 1996). Nowadays, the seven largest of the studied islands are inhabited. Signs of past human activity, such as abandoned cultivations and habitations, as well as seasonal or occasional grazing, are reported for most of the South Aegean islets (Höner & Greuter, 1988; Raus, 1989; Christodoulakis et al., 1991; Brullo & Guarino, 2000; Bergmeier et al., 2001; Panitsa et al., 2004).

The number of plant species hosted by 60 of the South Aegean islands was derived from seventeen available publications (see online supplementary material, Table S1). The flora of these 60 islands is well-known, recorded or revised between 1967 and 2006. Knowledge of Greek island flora is generally considered sufficient (see Greuter, 1995; Tzanoudakis & Panitsa, 1995). Some islets around Crete and Rodos, for which the floristic information available is still quite poor, and tiny non-vegetated rocky islets sporadically located close to large islands, were not considered in our analysis. Plants which were: (a) recorded in floristic inventories as cultivated or introduced but not naturalized, and (b) doubtfully present on the islands, with possibly dubious records or misidentified specimens, were not counted in the total number of species.

The area of the 60 islands ranged from $4.4 \times 10^{-4}$ to 8265 km$^2$. Forty-six islands have an area smaller than 1 km$^2$. We used island areas provided by the 1:50000 maps of the Greek Army Geographic Service. Some islets are referred to in the bibliography with more than one name, but we list here the most commonly used names, for simplicity (see online supplementary material, Table S1).

Species-area relationship

We applied the commonly used logarithmic transformation of the power function model (Arrhenius, 1921), i.e. $\log S = z \log A + \log c$ (Equation 1), for the total number of vascular species, and the endemics at different levels of endemism, namely, (a) single-island endemics, i.e. species endemic to a single island, (b) the South Aegean island arc endemics, (c) Aegean endemics, i.e. endemics shared among Aegean islands, and (d) total endemics, i.e. endemics shared between the South Aegean and the surrounding mainland Greece or Asia Minor, added to the sum of levels (a)-(c).

Additionally, we applied the standard linear regression model (Equation 1) to 51 of the South Aegean plant families. The remaining 75 plant families were not included in the analysis due to their limited number of species and/or the restricted number of islands where they occur. More specifically, among the 75 families: (a) 55 are either monotypical or comprise two to three species, which are also restricted to one to three islands, and (b) 20 families comprise one to four species, but they are represented by a single species on all islands where they occur, except on Crete, where all members of these families are present. For the comparison of parameters $c$ and $z$ of the regression lines, an Analysis of Covariance (ANCOVA) was performed.
Obtaining an adequate description of a habitat diversity-richness relationship requires that the habitat classification used reflects the natural history and ecological requirements of the taxon studied (Triantis et al., 2005, 2006). The definition and quantification of habitat diversity is an issue which calls for critical consideration (see discussion in Sfenthourakis & Triantis, 2009), and there is no commonly accepted description of plant habitat heterogeneity for Aegean islands. Following Yapp (1922), habitat is the dwelling place of a plant species, including all of the operative factors, except competition, that influence the plants themselves. Climatic and soil factors are among the essential operative measurable factors for habitat description (Fuller & Conard, 1983). We quantified habitat diversity according to a combination of four major habitat operative factors, namely light, temperature, moisture and soil salinity conditions, based on the Southern Aegean Indicator Values (SAIVs) of Böhling et al. (2002). The SAIVs provide a compact ecological characterization of 2242 South Aegean vascular plant taxa, and brings their ecological specialization to an operational mode (Böhling, 2004).

Based on the SAIVs scales of light, temperature and soil salinity we defined three types of habitats: (a) shady locations with lower temperatures and zero soil salinity, (b) semi-shady locations, with mild temperatures and mean soil salinity, and (c) locations fully exposed to sunlight, with higher temperatures and high soil salinity. Each one of the combinations described above was completed by one of the four levels of moisture conditions, from extremely dry locations to locations permanently or almost constantly under water (Böhling et al., 2002). Böhling (1994) and Böhling et al. (2002) defined moisture conditions after a simplified calculation of the plants water balance, considering precipitation and an indirect estimation of

### TABLE 1. An excerpt from the matrix of the flora of Kasos with the SAIVs of light (L), temperature (T), moisture (M) and salinity conditions (Sal), as given by Böhling et al. (2002). The lower values represent low intensities of a site factor, whereas the higher values are indicators of high intensities of a site factor. The symbol “X” indicates no particular or broad requirements for the respective environmental factor. Values marked with circle (e.g. 7Æ) indicate that the species requirements correspond mainly to the particular grade, but could be as broad as five grades

<table>
<thead>
<tr>
<th>Species</th>
<th>L</th>
<th>T</th>
<th>Sal</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allium ampeloprasum</td>
<td>8</td>
<td>7Æ</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Asphodelus ramosus ssp. ramosus (= “A. aestivus” = A. microcarpus Viv.)</td>
<td>8</td>
<td>X</td>
<td>1</td>
<td>3Æ</td>
</tr>
<tr>
<td>Atriplex halimus</td>
<td>8</td>
<td>8</td>
<td>3</td>
<td>X</td>
</tr>
<tr>
<td>Bromus madritensis s.l. (Anisantha madritensis s.l.)</td>
<td>7</td>
<td>X</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Capparis orientalis (C. spinosa ssp. rupestris)</td>
<td>9</td>
<td>8</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Carlina corymbosa s.l. (incl. C. graeca, C. curetum, C. sitiensis)</td>
<td>8</td>
<td>X</td>
<td>1</td>
<td>3Æ</td>
</tr>
<tr>
<td>Centaurea raphanina Sm. ssp. mixta</td>
<td>7</td>
<td>8</td>
<td>1</td>
<td>3Æ</td>
</tr>
<tr>
<td>Convolvulus oleifolius s.l.</td>
<td>8</td>
<td>8</td>
<td>1</td>
<td>3Æ</td>
</tr>
<tr>
<td>Cerdithymus capitatus (= Thymbra capitata (L.) Hoffmanns. &amp; Link = Thymbra capitata (L.) Cav.)</td>
<td>8</td>
<td>X</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Crepis multiflora</td>
<td>6</td>
<td>8</td>
<td>2</td>
<td>X</td>
</tr>
<tr>
<td>Crithmum maritimum</td>
<td>8</td>
<td>8</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Cynara cornigera (= C. sibthorpiana Boiss. &amp; Heldr.)</td>
<td>9</td>
<td>8</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Dactylis glomerata L. ssp. hispanica</td>
<td>7</td>
<td>7Æ</td>
<td>1</td>
<td>4Æ</td>
</tr>
<tr>
<td>Euphorbia dendroides</td>
<td>8</td>
<td>8</td>
<td>1</td>
<td>4Æ</td>
</tr>
<tr>
<td>Heliotropium dolosum</td>
<td>8</td>
<td>8</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Mesembryanthemum nodiflorum</td>
<td>9</td>
<td>8</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>Prasium majus</td>
<td>X</td>
<td>8</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Psilurus incurvus (P. aristatus)</td>
<td>7</td>
<td>7Æ</td>
<td>1</td>
<td>X</td>
</tr>
<tr>
<td>Sarcopoterium spinosum</td>
<td>8</td>
<td>7Æ</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Suaeda vera</td>
<td>8</td>
<td>8</td>
<td>5</td>
<td>X</td>
</tr>
<tr>
<td>Teucrium brevifolium</td>
<td>8</td>
<td>9</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Thymelaea hirsuta</td>
<td>8</td>
<td>8</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Urginea maritima (= Drimia maritima (L.) Stearn, Charybdis maritima s.l. incl. Ch. aphylla)</td>
<td>7</td>
<td>8Æ</td>
<td>1</td>
<td>2Æ</td>
</tr>
</tbody>
</table>
evapotranspiration according to air temperature (for discussion see Böhling, 1994). Some species are ecologically tolerant, thus occurring in more than one of habitats. The number of combinations of the above-defined habitats based on light, temperature, soil salinity and moisture conditions, which meets the requirements of all vascular plant species on each island, indicates the number of the island plant habitats. An example of habitat diversity counting according to SAIVs for the island of Kasos is presented in Tables 1-3.

Using this habitat diversity measure, we applied:
(a) The habitat diversity-species richness relationship, as a simple regression equivalent to Equation 1, substituting area for habitat diversity.

(b) The Choros model (Triantis et al., 2003), \( \log S = zK \log K + \log cK \), where \( K \) is the result of the multiplication of island size with the number of habitat types present on the island, and \( zK \) and \( cK \) are constants.

The best-fit model was determined by the Akaike Information Criterion (AIC) (Sakamoto et al., 1986; Li et al., 2002). If \( \Delta AIC = (AIC_{1st \ model} - AIC_{2nd \ model}) \) > 0, then the second model fits better with the data (Triantis et al., 2003).

Following the analysis of Panitsa et al. (2010), we examined island area, maximum elevation, shortest distance from the nearest mainland and from the nearest larger island, and habitat diversity as potential predictors of species diversity, using stepwise linear regression. Elevation and distances were provided by the 1:50000 maps of the Greek Army Geographic Service. Logarithmic transformation was applied to all variables. In order to avoid effects of colinearity among independent variables, we accepted only va-

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**Table 2.** The transformation of the SAIVs of light, temperature, soil salinity and moisture conditions in four or five levels, which were used in the present analysis, and the plants habitat traits that they represent

<table>
<thead>
<tr>
<th>Böhling et al. (2002) SAIVs</th>
<th>Level</th>
<th>Plant habitats traits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light (L)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-3</td>
<td>A</td>
<td>Shady</td>
</tr>
<tr>
<td>4-6</td>
<td>B</td>
<td>Semi-shady</td>
</tr>
<tr>
<td>7-9</td>
<td>C</td>
<td>Exposed to sunlight</td>
</tr>
<tr>
<td>X</td>
<td>X</td>
<td>Indifferent</td>
</tr>
<tr>
<td>Temperature (T)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-3</td>
<td>A</td>
<td>Low temperature</td>
</tr>
<tr>
<td>4-6</td>
<td>B</td>
<td>Mild temperature</td>
</tr>
<tr>
<td>7-9</td>
<td>C</td>
<td>High temperature</td>
</tr>
<tr>
<td>X</td>
<td>X</td>
<td>Indifferent</td>
</tr>
<tr>
<td>Soil salinity (Sal)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-2</td>
<td>A</td>
<td>No or very little soil salinity</td>
</tr>
<tr>
<td>3-5</td>
<td>B</td>
<td>Mild soil salinity</td>
</tr>
<tr>
<td>6-9</td>
<td>C</td>
<td>High soil salinity</td>
</tr>
<tr>
<td>X</td>
<td>X</td>
<td>Indifferent</td>
</tr>
<tr>
<td>Moisture conditions (M)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-3</td>
<td>A</td>
<td>Extremely dry</td>
</tr>
<tr>
<td>4-6</td>
<td>B</td>
<td>Semi-dry</td>
</tr>
<tr>
<td>7-9</td>
<td>C</td>
<td>Humid</td>
</tr>
<tr>
<td>10-12</td>
<td>D</td>
<td>Location permanently or almost continuously under water</td>
</tr>
<tr>
<td>X</td>
<td>X</td>
<td>Indifferent</td>
</tr>
</tbody>
</table>

**Table 3.** The habitat types resulting from the transformation of the SAIVs of the Kasos species listed in Table 1. Each habitat type is a combination of the level of light (L), temperature (T), soil salinity (Sal) and moisture conditions (M)

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>L</th>
<th>T</th>
<th>Sal</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>C</td>
<td>A</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>C</td>
<td>A</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>X</td>
<td>A</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>X</td>
<td>A</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>C</td>
<td>A</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>C</td>
<td>B</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>C</td>
<td>A</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>C</td>
<td>B</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>C</td>
<td>C</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td>Total: 10</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
riables with a tolerance value larger than 0.10 (Panit-
sa et al., 2010).
For all calculations, the statistical software STA-
TISTICA (version 6; Statsoft, Inc., Tulsa, OK, USA)
was used.

RESULTS
Species richness and parameter estimation
The total number of species occurring on the 60 is-
lands is 2313; 221 of them are endemic to the South
Aegean island arc (approximately 10% of the total
vascular flora). The plant species number per island
varied from 1 to 1795. Total vascular flora of the is-
lands, endemic species, habitat diversity and the val-
ues of other potential predictors of species richness
are presented in online supplementary material (Ta-
ble S1).

Total vascular flora of the 60 islands
There is a strong positive correlation between the va-
scular species number (S) and area (A) of the 60 is-
lands, with a correlation coefficient $r = 0.85$. The SAR
model as fitted explains 73% of the variability in spe-
cies richness (Table 4). However, the correlation was
stronger and the predictive power was higher when
habitats (H) and the Choros parameter ($K_{CH}$) were
regressed against species richness ($\Delta AICs = 12.5$
and 32.9, respectively). Comparing the Choros model to
the logS-logH regression, the second relationship was
more effective in describing species richness ($\Delta AIC$
= 20.5) (Table 4).

Colinearity was high between area and habitat di-
versity, therefore we ran each stepwise linear regres-
sion twice, each time using one of these variables.
Only the most effective significant models are pre-
presented in Table 5. Altitude (Alt), shortest distance
from continental area (DC) and habitat diversity en-
tered the regression for overall vascular flora of the
60 islands and this model explains 87% of the varia-
bility in species richness.

Endemic species
Among the SARs at different levels of endemism, the
South Aegean and Aegean ones are the weakest; the
simple regression model fitted explained 56% and

<table>
<thead>
<tr>
<th>Data set</th>
<th>Regression model</th>
<th>z</th>
<th>c</th>
<th>$R^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total vascular flora:</td>
<td>1. $\log S = z \log A + c$</td>
<td>0.39</td>
<td>2.01</td>
<td>0.73</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>60 islands</td>
<td>2. $\log S = z \log H + c$</td>
<td>2.24</td>
<td>-0.20</td>
<td>0.84</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>3$. $\log S = z \log (HA)$ + c</td>
<td>0.35</td>
<td>1.69</td>
<td>0.77</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Single island endemics (SI):</td>
<td>4. $\log E_{SI} = z \log A_{SI} + c$</td>
<td>0.71</td>
<td>-1.10</td>
<td>0.83</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>6 islands</td>
<td>5. $\log E_{SI} = z \log H_{SI} + c$</td>
<td>5.17</td>
<td>-6.63</td>
<td>0.75</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td></td>
<td>6$. $\log E_{SI} = z \log (H_{SI}A_{SI}) + c$</td>
<td>0.63</td>
<td>-1.78</td>
<td>0.82</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>South Aegean endemics (SA):</td>
<td>7. $\log E_{SA} = z \log A_{SA} + c$</td>
<td>0.15</td>
<td>0.26</td>
<td>0.56</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>24 islands</td>
<td>8. $\log E_{SA} = z \log H_{SA} + c$</td>
<td>1.14</td>
<td>-0.92</td>
<td>0.57</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>9$. $\log E_{SA} = z \log (H_{SA}A_{SA}) + c$</td>
<td>0.13</td>
<td>0.12</td>
<td>0.57</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Aegean endemics (AE):</td>
<td>10. $\log E_{AE} = z \log A_{AE} + c$</td>
<td>0.16</td>
<td>0.43</td>
<td>0.50</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>41 islands</td>
<td>11. $\log E_{AE} = z \log H_{AE} + c$</td>
<td>1.03</td>
<td>-0.59</td>
<td>0.48</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>12$. $\log E_{AE} = z \log (H_{AE}A_{AE}) + c$</td>
<td>0.15</td>
<td>0.28</td>
<td>0.51</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total endemics (TE):</td>
<td>13. $\log E_{TE} = z \log A_{TE} + c$</td>
<td>0.26</td>
<td>0.90</td>
<td>0.65</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>49 islands</td>
<td>14. $\log E_{TE} = z \log H_{TE} + c$</td>
<td>1.78</td>
<td>-0.89</td>
<td>0.72</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>15$. $\log E_{TE} = z \log (H_{TE}A_{TE}) + c$</td>
<td>0.23</td>
<td>0.67</td>
<td>0.68</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

* Choros Model
50% of the variability in endemic species richness, respectively (Table 4). For the six islands hosting single island endemics (Antikythira, Kythira, Gavdos, Crete, Karpathos and Rodos), the relationship with area is strong ($r = 0.91$) and the model is well-fitted ($R^2 = 0.83$); it also exhibits a high z-value ($z = 0.71$) (Table 4), which is higher than the upper limit of typical z-values for islands or isolated habitat patches (Rosenzweig, 2004).

In the case of single island endemics, the Choros model exhibits slightly lower descriptive power (Table 4) compared to the classic SAR ($\Delta AIC$ corrected for small sample sizes: $\Delta AICc = -0.13$), but higher than the species richness-habitat diversity model ($\Delta AICc = 2.19$). The stepwise linear regression indicated that among the examined potential predictors of species richness, only area is significant (Table 5).

The Choros model was more effective in explaining the numbers of the South Aegean (ESA), Aegean (EAE) and total endemics (ETE), compared to the SAR model ($\Delta AIC = 0.65$, 1.04 and 4.45, respectively), but less effective compared to the endemic species-habitat regression in the case of South Aegean endemics ($\Delta AIC = -0.07$) and of total endemics ($\Delta AIC = -5.57$) (Table 4).

Islands altitudes (Alt) and habitat types (H) jointly describe total endemics species richness in the South Aegean (ETE). The same parameters, together with nearest distance from continent (DC), depict more effectively the variability in Aegean endemics which occur in our study area (EA). As for South Aegean endemics, habitat diversity is the only significant parameter to explain variability in their area of distribution (Table 5).

**SARs at the family level**

Five of the 51 separate SARs at the family level have no statistically significant relationship between species numbers per family and area (for further details, see caption of online supplementary material, Table S2). These five families were represented by one species in most of the islands where they occur. Among the 46 families with statistically significant SARs, the number of species ranged from five (Aizoaceae and Verbanaceae) to 205 (Asteraceae), and the number of islands where the families were present ranged from five (Verbenaceae, Fagaceae and Saxifragaceae) to 54 (Fabaceae). The amount of variance of species richness explained by area ($R^2$) varied among plant families, from 40% (Araceae) to 92% (Cyperaceae). The family SARs varied significantly in relation to the size of each family (i.e. the total number of its representatives in South Aegean) and to its distributional range on the islands (online supplementary material, Table S2).

The values of the $c$-parameter regressed against species richness of each family in the study area showed a strong correlation; $c$-values increased with increasing family size, according to the equation:

$$c_{\text{Families}} = 0.07 S_{\text{Families}} + 0.49,$$

where $S_{\text{Families}}$ is the total species richness of each family in the South Aegean island arc.

The comparison of linear regressions using ANCOVA indicated that the SARs of 13 families exhibited $z$-values, which are not statistically different from the slope of the total vascular flora (online supplementary material, Table S2). All 46 $c$-values of the family SARs are significantly different from the intercept of the total SAR. The values of the $c$-parameter of the 13 families which exhibit $z$-values similar to that of the total SAR, regressed against the species richness of the same families, also showed a strong correlation; $c$-values increased with increasing family size, according to the equation:

\[c_{\text{Families}} = 0.07 S_{\text{Families}} + 0.49,\]

\[0.90 \text{ and } p < 0.01\]
the 13 families in the South Aegean island arc.

antis relationship (Lomolino, 2001; Tj
the pattern or the exact shape of this species-area re-
portance of individual mechanisms contributing to
theless, there is still no consensus concerning the im-
One almost always observes a positive correlation be-
species richness

where S13 Families is the total species richness of each of

DISCUSSION

Area, habitat diversity and other factors affecting plant
species richness

One almost always observes a positive correlation be-
tween species number and area, regardless of the cau-
sal mechanism (see Connor & McCoy, 1979). Never-
theless, there is still no consensus concerning the im-
portance of individual mechanisms contributing to
the pattern or the exact shape of this species-area re-

The South Aegean vascular plant SAR concurs
with the results of previous studies, where the area
was a significant explanatory variable of species rich-
ness. Kallimanis et al. (2010), applying the SAR for
plants of 201 islands of the Aegean Sea, identified is-
land area as the most important descriptor of the over-
all species richness. The SAR of plants in 86 East
Aegean islets, analyzed by Panitsa et al. (2006), was
statistically significant, but weak (R² = 0.323), and
had a steep slope, with z = 0.40. Therefore, although
the islands of this data set were all tiny (all < 0.050
km²), their plant communities conformed fairly well
to the traditional linearized power model and the rate
of increase in species number with area was similar to
the z-value of South Aegean islands. Numerous studies
in various archipelagos also indicated that, although
the mechanisms through which area determines the
number of species are still only partly understood, so
far area is the most powerful single explanatory vari-
able of species richness (e.g. MacArthur & Wilson,
1967; Rosenzweig, 1995; Delanoë et al., 1996; Whitt-
taker & Fernández-Palacios, 2007; Triantis et al.,
2008).

However, Panitsa et al. (2010) recently reported
that habitat diversity played an important role in
shaping most of the floral diversity patterns examined
in 20 East Aegean islands. The strong correlation be-
tween plant species richness and habitat diversity had
been documented earlier for other insular areas (e.g.
Deshay & Morisset, 1988; Kohn & Walsh, 1994).

Previous studies on some islands of the Aegean archi-
pelago and elsewhere had reported that substituting
area in the Arrhenius equation with the product of
habitat number and area (i.e. the Choros parameter)
resulted in a better prediction of species number (Tri-
ants et al., 2003, 2005; Panitsa et al., 2006; Hannus
& von Numers, 2008). Our results also stress the im-
portance of habitat diversity in determining the total vas-
cular flora of the 60 islands, the Aegean endemics
and the total endemics occurring in the South Aeg-
egan. The combination of habitat diversity and area,
as expressed by the Choros model (Triantis et al.,
2003), was most efficient in shaping the number of
South Aegean endemics.

Our definition of habitats, based on a transfor-
ation of Southern Aegean Indicator Values data (Böh-
ling et al., 2002) on light, temperature, moisture and
soil salinity, considered some major operative factors
which characterize plant habitats. Climatic, edaphic
and physiographic factors have been used in other
studies to define plant habitats (e.g. Deshay & Mor-
isset, 1988; Kohn & Walsh, 1994; Duarte et al.,
2008, Kreft et al., 2008). Nevertheless, no habitat definition
is all-embracing or broadly accepted (e.g. Deshay & Mor-
isset, 1988; Koh et al., 2002; Duarte et al., 2008;
Hannus & von Numers, 2008; Panitsa et al., 2010).
Despite dissimilar approaches to habitat diversity, re-
results concerning its role in shaping plant species rich-
ness tend to converge, because most of the habitat
definitions used reflect, more or less, topographic and
geological heterogeneity, which creates more habitat
types and thus promotes species richness, especially
when the species involved tend to be habitat special-
ists (Whittaker & Fernández-Palacios, 2007; Sfent-
hourakis & Triantis, 2009; Panitsa et al., 2010).

The sequential reduction of SARs R²-value, from
single island endemics to South Aegean and Aegean
endemics can be attributed to the more intense effect
of the idiosyncrasies of each island (e.g. area, isola-
tion, elevation) on its evolutionary dynamics. Thus,
although the realized total species carrying capacity of an island can usually be approximated by its area, for describing the island capacity in terms of endemism we have to consider the minimum area of specification or even more variables than just area. We should mention, though, that differences in fitted regression lines depend strongly on the data set used. Panitsa et al. (2006) and Kallimanis et al. (2010) concluded that other variables, especially maximum elevation, could play a more critical role than area. Legakis & Kypriotakis (1994) concluded that the combination of altitude and climate creates high habitat diversity in Crete, which partly justifies the high endemism on the island. In fact, 43% of Cretan endemics are found exclusively at altitudes higher than 1000 m (Legakis & Kypriotakis, 1994).

Our stepwise regressions indicated that the most prevailing factors influencing Aegean endemics in the South Aegean are altitude, the shortest distance from mainland and habitat diversity as defined through the SAIVs. The same parameters were significant in shaping the total vascular flora of the 60 islands. The "total endemics" are determined mainly by islands altitude and habitat diversity. Habitat diversity alone is sufficient in describing the number of South Aegean endemics. Altitude, which is a cause of habitat heterogeneity as well (Morrison, 1997; Fernández-Palacios & Andersson, 2000; Khedr & Lovett-Doust, 2000; Panitsa et al., 2006, 2010), contributes mostly to the prediction of species richness for total vascular flora and for most subsets of endemics. The role of habitat diversity for the endemic species is similar to that for total flora (Panitsa et al., 2010). Endemic species are not equally distributed among habitats; they tend to be concentrated in habitats where competition is low, due to high stress levels (e.g. cliffs, scree, rocky habitats) (Panitsa et al., 2010). As a result, more complex habitat heterogeneity affects their occurrence. The significance of the shortest distance from the mainland in shaping the total vascular flora and the Aegean endemics patterns indicates that the South Aegean islands are not detached from their neighbouring continent in terms of phytogeography. In fact, several of the South Aegean islands were connected to the mainland until Pleistocene (Sondaar, 1971; Meulenkamp et al., 1972; Daams & Van der Weerd, 1980; Beard et al., 1982; Dermitzakis, 1990). The patterns of single island endemics and South Aegean endemics are not affected by distance from mainland, because their populations are isolated, thus there is no or very little long-distance dispersal (see Cellinese et al., 2009). Our concept of “total endemics” integrated all categories of insular endemics (i.e. local, South Aegean and Aegean) together with endemics commonly distributed among the South Aegean arc and surrounding continental areas; therefore the effect of distance was eliminated. The distance from the nearest larger island did not enter any of the regressions, because most of the South Aegean islets are located close to the coasts of larger islands. In addition, distances among islands are not correlated with their habitat diversity.

Single-island endemics exhibit a strong relationship with area ($R^2 = 0.83$) and their number increases quickly with the increase in area (z = 0.71). Area per se is adequate for the description of their pattern in the South Aegean, whereas maximum elevation, shortest distance from the nearest mainland and from the nearest large island, as well as habitat diversity were not significant predictors. There is no satisfactory explanation why area is the sole predictor of single-island endemics. In contrast to this result, Panitsa et al. (2010) had found that habitat diversity, instead of area, was the only significant predictor of single-island endemics. This inconsistency in the results could be due to the different approaches to habitat diversity.

Triantis et al. (2008) proposed that islands can be considered equivalent to biological provinces for single-island endemics. Theoretically, biogeographic provinces are large enough and isolated, with the speciation rates far exceeding immigration rates, and z-values of 0.55-1.00 being observed among them (Rozensweig, 1995, 2003). An increase in area enhances the probabilities of in situ speciation (Lomolino & Wiiser, 2001; Duarte et al., 2008; Losos & Ricklefs, 2009). Available evidence on local endemics in the South Aegean indicates some cases of in situ speciation; Greuter (1972) stated that the endemic mountain flora of Crete consists mainly of derivatives of lowland species and of a small number of old relics (see also Legakis & Kypriotakis, 1994). A relatively high number of single-island endemics arose mainly through allopatric speciation across the different islands triggered by the (palaeo)geographic complexity of the Aegean region, and is not within-island (adaptive) speciation (see Critopoulos, 1975; Montmollin, 1991; Bittkau & Comes, 2009). However, there are also few South Aegean single-island endemics which are actually paleo-endemics, relics-survivors of the flora before isolation, such as Zelkova abelicea (Lam.) Boiss. (Ulmaceae), which is widely disjunct from its nearest relatives. Cellinese et al. (2009) performed a phyloge-
netic reconstruction of Campanulaceae species occurring on Crete and Karpathos. They found that most Cretan endemics of the family were present on the islands at the time of their isolation, and very little long-distance dispersal to Crete and diversification within Crete occurred since. Endemism of the family is probably driven by loss of species on the mainland after island isolation. Species on the islands may have been more widespread in the past, but they are now restricted to often inaccessible areas, probably as a result of human pressure.

In conclusion, our results demonstrate the significance of habitat diversity in interpreting variability in species richness and are in accordance with Panitsa et al. (2010), who also found that the Choros model is not a better predictor of richness than habitat alone. However, the effect of area on single island endemics shows that both area and habitat diversity should be examined for a more thorough interpretation of richness patterns. The different approaches to habitat diversity in various studies are a serious issue, which does not permit objective comparisons of the results concerning its significance in shaping species richness.

SARs at the family level

The family species-area patterns are shaped by family size, i.e. its total number of species in the South Aegean, and by the broadness of its distribution, i.e. the number and size of the islands where it occurs. For instance, families Aizoaceae and Verbenaceae comprised each of five species in total. However, Aizoaceae is widely distributed in 37 islands, thus exhibiting a very low z-value (0.08). On the other hand, Verbenaceae are found only on five large islands, where their damp habitats occur; therefore its z-value is higher.

The group of family SARs with z-values 0.08-0.24 gathers families with complex patterns that cannot be easily explained, as well as three families to which most of the halophytes belong, namely Plumbaginaceae, Chenopodiaceae and Juncaceae. Being mostly restricted in the littoral zone, halophytic species de facto have their habitats available on small and large islands. Long-distance dispersal constitutes a rather common feature among shore plants (Greuter, 1972). In general, species-area studies for littoral or shore plant communities show low z-values (Nilsson & Nilsson, 1978; Buckley, 1985; Deshaye & Morisset, 1988; Roden, 1998). The plant communities that inhabit the perimeters of islands comprise the largest proportion of the species that could potentially colonize these areas (Roden, 1998).

The highest z-values are observed for the families that comprise numerous and, as a rule, herbaceous species, namely Asteraceae, Brassicaceae, Apiaceae, Caryophyllaceae, Poaceae and Fabaceae, and occur on the majority of the islands. Many of these species are cosmopolitan, ruderal or weedy and widely distributed in various habitats, from sea level to the high mountains of Crete. Our results are in agreement with those of Roos et al. (2004), who found that some families exhibited higher z-values than the overall flora of Malesian islands. They also found that some families exhibit complex species-area patterns, which cannot be interpreted without recourse to some historical biogeographic explanation. In addition, specific diversity patterns are created by evolutionary processes, spatial interactions and the geographic, ecological and historic specificity of each region, and are also influenced by a number of incompletely known factors (Duarte et al., 2008).

Parameters z and c of the species-area relationship

Despite numerous biogeographic studies, few scientists have explored the central tendencies and biologically relevant variations in c-values. Gould (1979) proposed that the density of organisms, the number of species in higher taxa, the degree of isolation and the scale on which area is measured, affect the value of the c-parameter in various ways. Gould (1979) concluded that “in fact, so much variation is sopped up by c that particular values of it are hardly ever discussed”. Sfenthourakis (1996) also concluded that z- and c-values seem to be statistical artefacts which emerge from several intervening factors, such as the data set size and range. Lyons & Willig (1999) provided some insights into the geographic variation of both z and c. They compared cumulative species-area curves for mammals sampled across nested plots within latitudinal bands of North and South America. The pattern emerging from these studies is that, along a gradient from the equator to the poles, z-values increase while c-values decrease. Nevertheless, traditionally, c is considered as an indicator of the capacity of the area under study to support individuals and species (MacArthur & Wilson, 1967; Connor & McCoy, 1979; Brown & Lomolino, 1998), but, so far, there is not enough evidence supporting this view.

Our analysis revealed a strong correlation between the c-value and the 46 family species richness;
c-values increased with an increase in family species richness. This result indicates that the variation in c-values depends on family size. The general trend is that the most species-rich families exhibit the highest c-values (see online supplementary material, Table S2). At unit area (A = 1), logS is equal to logc, therefore the parameter c can be used as a proxy of a diversity measure. Nevertheless, according to the Arrhenius equation, c is also dependent on the z-parameter. Therefore, c is a diversity measure which can be used comparatively only for SARs which exhibit equal or statistically similar slopes. The c-values of the 13 family SARs with slopes similar to that of the total SAR are also strongly correlated with the 13 family species richness in the South Aegean. Moreover, the c-value for total vascular flora is much higher than that of any family. These results can be considered to support the ecological view of the c-parameter as an indicator of the capacity of the studied area; the larger the species pool, the higher the number of species that can be found within the measuring unit of area.

Species richness is a generalized variable. Therefore, a “deconstructive approach”, which disaggregates species richness into subsets of species with a common trait, can give better insights in the species-area pattern. In fact, such a deconstruction through the analysis of endemic species and family species numbers against area, proved quite informative.

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