

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

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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.

### INTRODUCTION

The South Aegean island arc is an archipelago of extreme botanical interest, as it hosts more than 2300 species and subspecies of vascular plants (Böhling *et al.*, 2002). Moreover, its high degree of plant endemism, compared to that of other parts of the Aegean archipelago, was one of the criteria for its designation

as a phytogeographical unit by Rechinger & Rechinger-Moser (1951). Therefore, the South Aegean is ideal for the investigation of native and endemic plant species richness patterns. Since the beginning of the 19<sup>th</sup> century, the geographic position, geological dynamics and high endemism of this archipelago have spawned a large number of studies focusing on its floristic relationships with neighboring continental areas (Rechinger & Rechinger-Moser, 1951; Greuter, 1971; Carlström, 1987; Raus, 1991; Strid, 1996), its floristic unity and alternative phytogeographical divisions

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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 & Kypriotakis, 1994; Bergmeier & Dimopoulos, 2003; Kalilimanis *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 biogeographic 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 *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

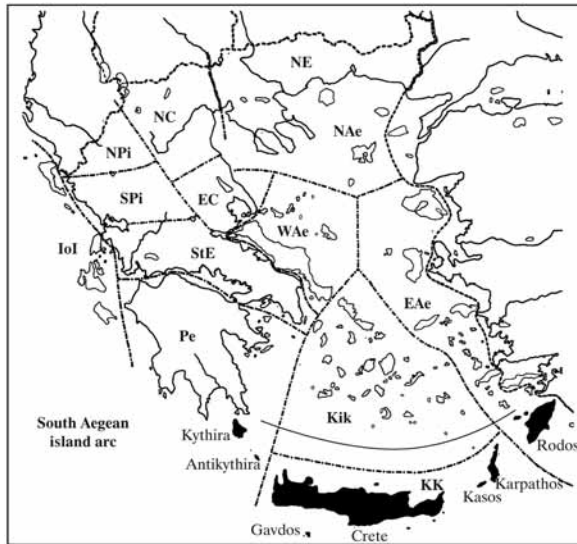


FIG. 1. The floristic regions of Greece and the South Aegean island arc, from Kythira to Rodos. Kythira and Antikythira are also floristically related with Peloponissos (Pe) and Rodos is also related with East Aegean islands (EAe). Gavdos, Kasos and Karpathos have some major floristic similarities with Crete and they constitute together the central part of the South Aegean island arc (KK) (from Strid & Tan, 1997, modified).

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  $\sim 37$  km away from Crete and  $\sim 250$  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<sup>2</sup>. Forty-six islands have an area smaller than 1 km<sup>2</sup>. 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.

*Potential predictors of species richness*

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. 7°) indicate that the species requirements correspond mainly to the particular grade, but could be as broad as five grades

Species	L	T	Sal	M
<i>Allium ampeloprasum</i>	8	7°	1	4
<i>Asphodelus ramosus</i> ssp. <i>ramosus</i> (= “ <i>A. aestivus</i> ” = <i>A. microcarpus</i> Viv.)	8	X	1	3°
<i>Atriplex halimus</i>	8	8	3	X
<i>Bromus madritensis</i> s.l. ( <i>Anisantha madritensis</i> s.l.)	7	X	1	4
<i>Capparis orientalis</i> ( <i>C. spinosa</i> ssp. <i>rupestris</i> )	9	8	3	1
<i>Carlina corymbosa</i> s.l. (incl. <i>C. graeca</i> , <i>C. curetum</i> , <i>C. sitiensis</i> )	8	X	1	3°
<i>Centaurea raphanina</i> Sm. ssp. <i>mixta</i>	7	8	1	3°
<i>Convolvulus oleifolius</i> s.l.	8	8	1	3°
<i>Coridothymus capitatus</i> (= <i>Thymus capitatus</i> (L.) Hoffmanns. & Link = <i>Thymbra capitata</i> (L.) Cav.)	8	X	1	3
<i>Crepis multiflora</i>	6	8	2	X
<i>Crithmum maritimum</i>	8	8	5	2
<i>Cynara cornigera</i> (= <i>C. sibthorpiana</i> Boiss. & Heldr.)	9	8	2	2
<i>Dactylis glomerata</i> L. ssp. <i>hispanica</i>	7	7°	1	4°
<i>Euphorbia dendroides</i>	8	8	1	4°
<i>Heliotropium dolosum</i>	8	8	1	5
<i>Mesembryanthemum nodiflorum</i>	9	8	9	1
<i>Prasium majus</i>	X	8	1	3
<i>Psilurus incurvus</i> ( <i>P. aristatus</i> )	7	7°	1	X
<i>Sarcopoterium spinosum</i>	8	7°	1	4
<i>Suaeda vera</i>	8	8	5	X
<i>Teucrium brevifolium</i>	8	9	1	2
<i>Thymelaea hirsuta</i>	8	8	1	4
<i>Urginea maritima</i> (= <i>Drimia maritima</i> (L.) Stearn, <i>Charybdis maritima</i> s.l. incl. <i>Ch. aphylla</i> )	7	8°	1	2°

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

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

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),  $\log S = z_K \log K + \log c_K$ , where K is the result of the multiplication of island size with the number of habitat types present on the island, and  $z_K$  and  $c_K$  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

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)

Habitat type			
L	T	Sal	M
X	C	A	A
B	C	A	X
C	X	A	A
C	X	A	B
C	C	A	X
C	C	B	X
C	C	A	A
C	C	A	B
C	C	B	A
C	C	C	A
Total: 10			

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 collinearity among independent variables, we accepted only va-

riables with a tolerance value larger than 0.10 (Panitza et al., 2010).

For all calculations, the statistical software STATISTICA (version 6; Statsoft, Inc., Tulsa, OK, USA) was used.

## RESULTS

### Species richness and parameter estimation

The total number of species occurring on the 60 islands 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 islands, endemic species, habitat diversity and the values of other potential predictors of species richness are presented in online supplementary material (Table S1).

### Total vascular flora of the 60 islands

There is a strong positive correlation between the vascular species number (S) and area (A) of the 60 islands, with a correlation coefficient  $r = 0.85$ . The SAR

model as fitted explains 73% of the variability in species richness (Table 4). However, the correlation was stronger and the predictive power was higher when habitats (H) and the Choros parameter ( $K_H$ ) 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 diversity, therefore we ran each stepwise linear regression twice, each time using one of these variables. Only the most effective significant models are presented in Table 5. Altitude (Alt), shortest distance from continental area (DC) and habitat diversity entered the regression for overall vascular flora of the 60 islands and this model explains 87% of the variability 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 4. Regression models fitted, their parameters  $z$  and  $c$ , determination coefficients ( $R^2$ ) and significance ( $p$ ) for predicting: the total number of vascular plant species (S), the number of single island endemics ( $E_{SI}$ ), the number of South Aegean endemics ( $E_{SA}$ ), the number of Aegean endemics ( $E_{AE}$ ), and the number of total endemics ( $E_{TE}$ ). Predictor variables are: islands area (A, in  $km^2$ ), number of habitats on islands hosting the respective category of endemic species (H) and the product HA (Choros parameter)

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

\* Choros Model

TABLE 5. Results of stepwise linear regressions. Alt: maximum altitude; DC: shortest distance from nearest mainland; H: number of habitats according to Southern Aegean Indicator Values for light, temperature, moisture and soil salinity. The indicators “AE” and “TE” refer to Aegean endemics and total endemics, respectively

Data set	Regression model	R <sup>2</sup>
Total vascular flora	$\log S = 0.21 \log(\text{Alt}) + 0.36 \log(\text{DC}) + 1.93 \log H - 0.31$	0.87
Single island endemics	Reduced to simple regression 4 in Table 4	
South Aegean endemics	Reduced to simple regression 8 in Table 4	
Aegean endemics	$\log E_{\text{AE}} = 0.34 \log(\text{Alt}_{\text{AE}}) + 0.53 \log(\text{DC}_{\text{AE}}) + 0.57 \log H_{\text{AE}} - 0.87$	0.65
Total endemics	$\log E_{\text{TE}} = 0.25 \log(\text{Alt}_{\text{TE}}) + 1.26 \log H_{\text{TE}} - 0.09$	0.76

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 ( $\Delta\text{AICc} = -0.13$ ), but higher than the species richness-habitat diversity model ( $\Delta\text{AICc} = 2.19$ ). 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 ( $E_{\text{SA}}$ ), Aegean ( $E_{\text{AE}}$ ) and total endemics ( $E_{\text{TE}}$ ), compared to the SAR model ( $\Delta\text{AIC} = 0.65, 1.04$  and  $4.45$ , respectively), but less effective compared to the endemic species-habitat regression in the case of South Aegean endemics ( $\Delta\text{AIC} = -0.07$ ) and of total endemics ( $\Delta\text{AIC} = -5.57$ ) (Table 4).

Islands altitudes (Alt) and habitat types (H) jointly describe total endemics species richness in the South Aegean ( $E_{\text{TE}}$ ). The same parameters, together with nearest distance from continent (DC), depict more effectively the variability in Aegean endemics which occur in our study area ( $E_{\text{AE}}$ ). 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 spe-

cies 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:

$$c_{\text{Families}} = 0.07 S_{\text{Families}} + 0.49, \text{ with } R^2 = 0.90 \text{ and } p < 0.01$$

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:

$$c_{13 \text{ Families}} = 0.07 S_{13 \text{ Families}} - 0.31,$$

with  $R^2 = 0.95$  and  $p < 0.01$

where  $S_{13 \text{ Families}}$  is the total species richness of each of the 13 families in the South Aegean island arc.

## DISCUSSION

### *Area, habitat diversity and other factors affecting plant species richness*

One almost always observes a positive correlation between species number and area, regardless of the causal mechanism (see Connor & McCoy, 1979). Nevertheless, there is still no consensus concerning the importance of individual mechanisms contributing to the pattern or the exact shape of this species-area relationship (Lomolino, 2001; Tjørve, 2003, 2009; Triantis *et al.*, 2003; Whittaker & Fernández-Palacios, 2007; Dengler, 2009). In the present study, species richness and area are strongly related for all diversity metrics used, namely the total vascular species richness, the endemism and the richness of each family. The slope of the SAR indicates the rate of increase of species richness with area and it varies with the geographic unit and the taxonomic group analyzed (MacArthur & Wilson, 1967; Malyshev, 1991; Duarte *et al.*, 2008). In our case, the SARs z-value (0.39) is consistent with the higher floristic heterogeneity values observed in isolated floras, as it falls within the range of 0.2-0.5 proposed by Rosenzweig (1995) for island groups or isolated habitat patches [see also Hobohm (2000) for a number of archipelagos around the world].

The South Aegean vascular plant SAR concurs with the results of previous studies, where the area was a significant explanatory variable of species richness. Kallimanis *et al.* (2010), applying the SAR for plants of 201 islands of the Aegean Sea, identified island area as the most important descriptor of the overall species richness. The SAR of plants in 86 East Aegean islets, analyzed by Panitsa *et al.* (2006), was statistically significant, but weak ( $R^2 = 0.323$ ), and had a steep slope, with  $z = 0.40$ . Therefore, although the islands of this data set were all tiny (all  $< 0.050 \text{ km}^2$ ), 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 variable of species richness (e.g. MacArthur & Wilson, 1967; Rosenzweig, 1995; Delanoë *et al.*, 1996; Whittaker & 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 between plant species richness and habitat diversity had been documented earlier for other insular areas (e.g. Deshayé & Morisset, 1988; Kohn & Walsh, 1994). Previous studies on some islands of the Aegean archipelago 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 (Triantis *et al.*, 2003, 2005; Panitsa *et al.*, 2006; Hannus & von Numers, 2008). Our results also stress the importance of habitat diversity in determining the total vascular flora of the 60 islands, the Aegean endemics and the total endemics occurring in the South Aegean. 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 transformation of Southern Aegean Indicator Values data (Böhling *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. Deshayé & Morisset, 1988; Kohn & Walsh, 1994; Duarte *et al.*, 2008; Kreft *et al.*, 2008). Nevertheless, no habitat definition is all-embracing or broadly accepted (e.g. Deshayé & Morisset, 1988; Koh *et al.*, 2002; Duarte *et al.*, 2008; Hannus & von Numers, 2008; Panitsa *et al.*, 2010). Despite dissimilar approaches to habitat diversity, results concerning its role in shaping plant species richness 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 specialists (Whittaker & Fernández-Palacios, 2007; Sfenthourakis & Triantis, 2009; Panitsa *et al.*, 2010).

The sequential reduction of SARs  $R^2$ -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, isolation, 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 speciation 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, screes, 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; Meulenkaamp *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 (Rosenzweig, 1995, 2003). An increase in area enhances the probabilities of *in situ* speciation (Lomolino & Weiser, 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; Deshayé & Morisset, 1988; Roden, 1998). The plant communities that inhabit the perimeters of islands comprise the largest propor-

tion 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 ( $A = 1$ ),  $\log S$  is equal to  $\log c$ , 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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#### REFERENCES

- Arrhenius O, 1921. Species and area. *Journal of Ecology*, 9: 95-99.
- Beard JH, Sangree JB, Smith LA, 1982. Quaternary chronology, paleoclimate, depositional sequences and eustatic cycles. *American Association of Petroleum Geologists Bulletin*, 66: 158-169.
- Bergmeier E, 2002. The vegetation of the high mountains of Crete—a revision and multivariate analysis. *Phytocoenologia*, 32: 205-249.
- Bergmeier E, Dimopoulos P, 2001. Chances and limits of floristic island inventories—the Dionysades group (South Aegean, Greece) re-visited. *Phyton-Annales Rei Botanicae*, 41: 277-293.
- Bergmeier E, Dimopoulos P, 2003. The vegetation of islets in the Aegean and the relation between the occurrence of islet specialists, island size, and grazing. *Phytocoenologia*, 33: 447-474.
- Bergmeier E, Jahn R, Jagel A, 1997. Flora and vegetation of Gavdos (Greece), the southernmost European island. I. Vascular flora and chorological relations. *Candollea*, 52: 305-358.
- Bergmeier E, Kypriotakis Z, Jahn R, Böhling N, Dimopoulos P, Raus T, Tzanoudakis D, 2001. Flora and phytogeographical significance of the islands Chrysi, Koufonisi and nearby islets (S Aegean, Greece). *Willdenowia*, 31: 329-356.
- Bittkau C, Comes HP, 2009. Molecular inference of a Late Pleistocene diversification shift in *Nigella* s. lat. (Ranunculaceae) resulting from increased speciation in the Aegean archipelago. *Journal of Biogeography*, 36: 1346-1360.
- Böhling NB, 1994. *Studien zur landschaftsökologischen Raumgliederung auf der mediterranen Insel Naxos (Griechenland); unter besonderer Berücksichtigung von Zeigerpflanzen. Dissertationes Botanicae*, 230. J Cramer Verlag, Berlin, Stuttgart.
- Böhling N, 2004. Southern Aegean indicator values – Derivation, application and perspectives. In: Arianoutsou M, Papanastasis V, eds. *Proceedings of the 10<sup>th</sup> MEDE-COS Conference*, Rhodes, Greece. Millpress, Rotterdam: 1-13.
- Böhling N, Greuter W, Raus T, 2002. Indicator values of the vascular plants in the Southern Aegean (Greece). *Braun-Blanquetia*, 32: 1-106.
- Brown JH, Lomolino MV, 1998. *Biogeography*. Sinauer Associates, Sunderland.
- Brullo S, Guarino R, 2000. Contribution to the knowledge of flora and vegetation of Khrisi islet (Crete, SE Mediterranean sea). *Flora Mediterranea*, 10: 265-282.
- Buckley RC, 1985. Distinguishing the effects of area and habitat type on island plant species richness by separating floristic elements and substrate types and controlling for island isolation. *Journal of Biogeography*, 12: 527-535.
- Carlström A, 1986. New taxa and notes from the SE Aegean area and SW Turkey. *Willdenowia*, 16: 73-78.
- Carlström A, 1987. *A survey of the Flora and Phytogeography of Rodhos, Simi, Tilos and the Marmaris peninsula (SE Greece, SW Turkey)*. Ph.D. Thesis, University of Lund.
- Cellinese N, Smith SA, Edwards EJ, Kim S-T, Haberle RC, Avramakis M, Donoghue MJ, 2009. Historical biogeography of the endemic Campanulaceae of Crete. *Journal of Biogeography*, 36: 1253-1269.
- Chilton L, 2002. *Plant list for Rhodes*. Marengo Publications.
- Chilton L, 2003. *Plant list for Karpathos*. Marengo Publications.
- Christodoulakis D, Georgiadis Th, Economidou E, Iatrou

- G, Tzanoudakis D, 1990. Flora und Vegetation der Diosynaden-Inseln (Südägäis, Griechenland). *Willdenowia*, 19: 425-443.
- Christodoulakis D, Economidou E, Georgiadis T, 1991. Geobotanische Studie der Grabusen-Inseln (Südägäis-Griechenland). *Botanica Helvetica*, 101: 53-67.
- Connor EF, McCoy ED, 1979. The statistics and biology of the species-area relationship. *American Naturalist*, 113: 791-833.
- Crawley MJ, Harral JE, 2001. Scale dependence in plant biodiversity. *Science*, 291: 864-868.
- Critopoulos P, 1975. The endemic taxa of Crete. In: Jordanov D, ed. *Problems of Balkan Flora and Vegetation. Proceedings of the First International Symposium on Balkan Flora and Vegetation, Varna, June 7-14 1973*. Bulgarian Academy of Sciences, Sofia: 169-177.
- Daams R, van der Weerd A, 1980. Early Pliocene small mammals from the Aegean island of Karpathos (Greece) and their palaeogeographic significance. *Geologie en Mijnbouw*, 59: 327-331.
- Delanoë O, Montmollin de B, Olivier L, 1996. *Conservation of the Mediterranean Island Plants: I. Strategy for Action*. IUCN, Gland and Cambridge.
- Dengler J, 2009. Which function describes the species-area relationship best? A review and empirical evaluation. *Journal of Biogeography*, 36: 728-744.
- Dermitzakis DM, 1990. Paleogeography, geodynamic processes and event stratigraphy during the Late Cenozoic of the Aegean Area. *International Symposium on: Biogeographical Aspects of Insularity. Roma, Accademia Nazionale dei Lincei*, 85: 263-288.
- Deshaye J, Morisset P, 1988. Floristic richness, area, and habitat diversity in a hemiarctic archipelago. *Journal of Biogeography*, 15: 747-757.
- Duarte MC, Rego F, Romeiras MM, Moreira I, 2008. Plant species richness in the Cape Verde islands – eco-geographical determinants. *Biodiversity and Conservation*, 17: 453-466.
- Fattorini S, 2007. To fit or not to fit? A poorly fitting procedure produces inconsistent results when the species-area relationship is used to locate hotspots. *Biodiversity and Conservation*, 16: 2531-2538.
- Fernández-Palacios JM, Andersson C, 2000. Geographical determinants of the biological richness in the Macaronesian region. *Acta Phytogeographica Suecica*, 85: 41-50.
- Fuller GD, Conard HS, 1983. *Plant Sociology. The study of plant communities*. Koeltz Scientific Books, Koenigstein.
- Gehu JM, Apostolides N, Gehu-Franck J, Arnold K, 1989. Premières données sur la végétation littorale des îles de Rodhos et de Karpathos (Grèce). *Colloques phytosociologiques, XIX, Végétation et qualité de l'environnement côtier en Méditerranée*: 545-582.
- Gould SJ, 1979. An allometric interpretation of species-area curves: The meaning of the coefficient. *American Naturalist*, 114: 335-343.
- Greuter W, 1970. Zur Paläogeographie und Florengeschichte der südlichen Ägäis. *Feddes Repertorium*, 81: 233-242.
- Greuter W, 1971. Betrachtungen zur Pflanzengeographie der Südägäis. *Opera Botanica*, 30: 49-64.
- Greuter W, 1972. The relict element of the flora of Crete and its evolutionary significance. In: Valentine DH, ed. *Taxonomy, phytogeography and evolution*. Academic Press, London: 161-177.
- Greuter W, 1991. Botanical diversity, endemism, rarity, and extinction in the Mediterranean area: an analysis based on the published volumes of Med-Checklist. *Botanica Chronika*, 10: 63-79.
- Greuter W, 1995. Origin and peculiarities of Mediterranean island floras. *Ecologia Mediterranea*, 21: 1-10.
- Greuter W, Rechinger KH, 1967. Flora der Insel Kythera, gleichzeitig Beginn einer nomenklatorischen Überprüfung der griechischen Gefäßpflanzenarten. *Boissiera*, 13.
- Greuter W, Pleger R, Raus T, 1983. The vascular flora of the Karpathos island group (Dodecanesos, Greece). A preliminary checklist. *Willdenowia*, 13: 43-78.
- Hannus JJ, von Numers M, 2008. Vascular plant species richness in relation to habitat diversity and island area in the Finnish Archipelago. *Journal of Biogeography*, 35: 1077-1086.
- He F, Legendre P, 1996. On species-area relations. *American Naturalist*, 148: 719-737.
- Hobohm C, 2000. Plant species diversity and endemism on islands and archipelagos, with special reference to the Macaronesian Islands. *Flora*, 195: 9-24.
- Höner D, 1990. Mehrjährige Beobachtungen kleiner Vegetationsflächen im Raume von Karpathos (Nomos Dodekanisou, Griechenland). Ein Beitrag zur Klärung des „Kleininselpänomens“. *Dissertationes Botanicae*, 173: 1-185.
- Höner D, Greuter W, 1988. Plant population dynamics and species turnover on small islands near Karpathos (South Aegean, Greece). *Vegetatio*, 77: 129-137.
- Hortal J, Triantis KA, Meiri S, Thébault E, Sfenthourakis S, 2009. Island species richness increases with habitat diversity. *American Naturalist*, 174: 205-217.
- Huston M, 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.
- Iatrou G, 1994. The endemic flora of the island of Kythira. *Proceedings of the 5th Congress of the Hellenic Botanical Society*: 213 (in greek).
- Jahn R, Schönfelder P, 1995. *Exkursionsflora für Kreta*. Eugen Ulmer, Stuttgart.
- Kallimanis AS, Bergmeier E, Panitsa M, Georghiou K, Delipetrou P, Dimopoulos P, 2010. Biogeographical determinants for total and endemic species richness in a continental archipelago. *Biodiversity and Conservation*,

- 19: 1225-1235.
- Khedr AH, Lovett-Doust J, 2000. Determinants of floristic diversity and vegetation composition on the islands of Lake Burollos, Egypt. *Applied Vegetation Science*, 3: 147-156.
- Koh LP, Sodhi NS, Tan HTW, Peh KSH, 2002. Factors affecting the distribution of vascular plants, springtails, butterflies and birds on small tropical islands. *Journal of Biogeography*, 29: 93-108.
- Kohn DD, Walsh DM, 1994. Plant species richness – the effect of island size and habitat diversity. *Journal of Ecology*, 82: 367-377.
- Kreft H, Jetz W, Mutke J, Kier G, Barthlott W, 2008. Global diversity of island floras from a macroecological perspective. *Ecology Letters*, 11: 116-127.
- Legakis A, Kyriotakis Z, 1994. A biogeographic analysis of the island of Crete (Greece). *Journal of Biogeography*, 21: 441-445.
- Li B, Morris J, Martin EB, 2002. Model selection for partial least squares regression. *Chemometrics and Intelligent Laboratory Systems*, 64: 79-89.
- Lomolino MV, 2001. The species-area relationship: new challenges for an old pattern. *Progress in Physical Geography*, 25: 1-21.
- Lomolino MV, Weiser MD, 2001. Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography*, 28: 431-445.
- Losos JB, Ricklefs RE, 2009. Adaptation and diversification on islands. *Nature*, 457: 830-836.
- Lyons SK, Willig MR 1999. A hemispheric assessment of scale dependence in latitudinal gradients of species richness. *Ecology*, 80: 2483-2491.
- MacArthur RH, Wilson EO, 1967. *The theory of island biogeography*. *Monographs in Population Biology*. Princeton University Press, Princeton.
- Malyshev LI, 1991. Some quantitative approaches to problems of comparative floristics. In: Nimis PL, Crovello TJ, eds. *Quantitative approaches to phytogeography*. Kluwer Academic Publishers, Dordrecht, Boston, London: 15-33.
- Marquet PA, Fernández M, Navarrete SA, Valdovinos C, 2004. Diversity emerging: Toward a deconstruction of biodiversity patterns. In: Lomolino M, Heaney L, eds. *Frontiers of Biogeography: New directions in the Geography of Nature*. Cambridge University Press: 191-209.
- Meulenkamp JE, de Mulder EFJ, van der Weerd A, 1972. Sedimentary history and paleogeography of the late Cenozoic of the island of Rhodes. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 123: 541-553.
- Montmollin de B, 1991. Endémisme intra-cretois et trans-égéo-crétois – origine et différenciation. *Botanika Chronika*, 10: 125-135.
- Morrison LW, 1997. The insular biogeography of small Bahamian cays. *Journal of Ecology*, 85: 441-454.
- Nilsson SG, Nilsson IN, 1978. Species richness and dispersal of vascular plants to islands in lake Möckeln, Southern Sweden. *Ecology*, 59: 473-480.
- Panitsa M, Bazos I, Dimopoulos P, Zervou S, Yannitsaros A, Tzanoudakis D, 2004. Contribution to the study of the flora and vegetation of the Kithira island group: offshore islets of Kithira (S Aegean, Greece). *Willdenowia*, 34: 101-115.
- Panitsa M, Tzanoudakis D, Triantis K, Sfenthourakis S, 2006. Patterns of species richness on very small islands: the plants of the Aegean archipelago. *Journal of Biogeography*, 33: 1223-1234.
- Panitsa M, Trigas P, Iatrou G, Sfenthourakis S, 2010. Factors affecting plant species richness and endemism on land-bridge islands – An example from the East Aegean archipelago. *Acta Oecologica*, 36: 431-437.
- Rackham O, Moody J, 1996. *The making of the Cretan landscape*. Manchester University Press, Manchester.
- Raus T, 1989. Die Flora von Armathia und der Kleininseln um Kasos (Dodekanes, Griechenland). *Botanika Chronika*, 9: 19-39.
- Raus T, 1991. Asia or Europe? The phytogeographical position of the Karpathos archipelago (SE Aegean, Greece). *Flora et Vegetatio Mundi*, 9: 301-310.
- Raus T, 1996. Additions and amendments to the flora of the Karpathos island group (Dodekanesos, Greece). *Botanika Chronika*, 12: 21-53.
- Rechinger KH, Rechinger-Moser F, 1951. *Phytogeographia Aegaea*. Akademie der Wissenschaften Wien, Mathematische-Naturwissenschaftliche Klasse, Denkschrift. 105.
- Roden CM, 1998. Persistence, extinction, and different species pools within the flora of lake islands in western Ireland. *Journal of Biogeography*, 25: 301-310.
- Roos MC, Kessler PJA, Gradstein SR, Baas P, 2004. Species diversity and endemism of five major Malesian Islands: diversity-area relationships. *Journal of Biogeography*, 31: 1893-1908.
- Rosenzweig ML, 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rosenzweig ML, 2003. Reconciliation ecology and the future of species diversity. *Oryx*, 37: 194-205.
- Rosenzweig ML, 2004. Applying species-area relationships to the conservation of species diversity. In: Lomolino MV, Heaney LR, eds. *Frontiers of Biogeography: new directions in the geography of nature*. Sinauer Associates, Sunderland: 325-343.
- Sakamoto Y, Ishiguro M, Kitagawa G, 1986. *Akaike Information Criterion Statistics*. KTK Scientific Publishers, Tokyo.
- Scheiner SM, 2003. Six types of species-area curves. *Global Ecology and Biogeography*, 12: 441-447.
- Sfenthourakis S, 1996. The species-area relationship of terrestrial isopods (Isopoda; Oniscidea) from the Aegean archipelago (Greece): a comparative study. *Global Ecology and Biogeography Letters*, 5: 149-157.

- Sfenthourakis S, Triantis KA, 2009. Habitat diversity, ecological requirements of species and the Small Island Effect. *Diversity and Distributions*, 15: 131-140.
- Shmida A, Wilson MV, 1985. Biological determinants of species diversity. *Journal of Biogeography*, 12: 1-20.
- Simberloff D, 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics*, 19: 473-511.
- Sondaar PY, 1971. Paleozoogeography of the Pleistocene mammals from the Aegean. *Opera Botanica*, 30: 65-70.
- Strid A, 1996. Phytogeographia Aegaea and the Flora Hellenica Database. *Annalen der Naturhistorischen Museums in Wien*, 98: 279-289.
- Strid A, Tan K, 1997. *Flora Hellenica. Vol. 1*. Koeltz Scientific Books, Königstein, Germany.
- Tjørve E, 2003. Shapes and functions of species-area curves: a review of possible models. *Journal of Biogeography*, 30: 827-835.
- Tjørve E, 2009. Shapes and functions of species-area curves (II): a review of new models and parameterizations. *Journal of Biogeography*, 36: 1435-1445.
- Triantis KA, Mylonas M, Lika K, Vardinoyannis K, 2003. A model for the species-area-habitat relationship. *Journal of Biogeography*, 30: 19-27.
- Triantis KA, Mylonas M, Weiser MD, Lika K, Vardinoyannis K, 2005. Species richness, habitat diversity and area: A case study based on land snails in Skyros archipelago (Aegean Sea, Greece). *Journal of Biogeography*, 32: 1727-1735.
- Triantis KA, Vardinoyannis K, Tsolaki EP, Botsaris I, Lika K, Mylonas M, 2006. Re-approaching the small island effect. *Journal of Biogeography*, 33: 914-923.
- Triantis KA, Mylonas M, Whittaker RJ, 2008. Evolutionary species-area curves as revealed by single-island endemics: insights for the interprovincial species-area relationship. *Ecography*, 31: 401-407.
- Turland NJ, Chilton L, 1994. Studies on the Cretan flora 3. Additions to the flora of Karpathos. *Bulletin of the Natural History Museum of London (Botany Series)*, 24: 91-99.
- Tzanoudakis D, Panitsa M, 1995. The flora of the Greek islands. *Ecologia Mediterranea*, 21: 195-212.
- Tzanoudakis D, Iatrou G, Panitsa M, Trigas P, 1998. Contribution to the study of the Greek insular flora: Antikythera and the islets around Kythera. In: Tsekos I, Moustakas M, eds. *Progress in Botanical Research*. Proceedings of the 1<sup>st</sup> Balkan Botanical Congress. Kluwer Academic Publishers, Dordrecht: 177-180.
- Tzanoudakis D, Panitsa M, Trigas P, Iatrou G, 2006. Floristic and phytosociological investigation of the island Antikythera and nearby islets (SW Aegean, Greece). *Willdenowia*, 36: 1-17.
- Whittaker RJ, Fernández-Palacios JM, 2007. *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.
- Williams MR, Lamont BB, Henstridge JD, 2009. Species-area functions revisited. *Journal of Biogeography*, 36: 1994-2004.
- Yannitsaros A, 1969. *Contribution to the knowledge of the flora and vegetation of the island of Kythera*. Ph.D. Thesis, University of Athens (in Greek).
- Yannitsaros A, 1998. Additions to the flora of Kithira (Greece) I. *Willdenowia*, 28: 77-94.
- Yannitsaros A, 2004. Additions to the flora of Kithira (Greece) II. *Willdenowia*, 34: 117-128.
- Yapp RH, 1922. The concept of habitat. *Journal of Ecology*, 1: 1-17.
- Zaffran J, 1990. *Contributions à la flore et à la végétation de la Crète*. Publications de l'Université de Provence, Aix en Provence.
- Zohary M, Orshan G, 1965. An outline of the geobotany of Crete. *Israel Journal of Botany*, 14: 1-49.