



# Patterns of species richness on very small islands: the plants of the Aegean archipelago

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## ABSTRACT

**Aim** To investigate the species–area relationship (SAR) of plants on very small islands, to examine the effect of other factors on species richness, and to check for a possible Small Island Effect (SIE).

**Location** The study used data on the floral composition of 86 very small islands (all < 0.050 km<sup>2</sup>) of the Aegean archipelago (Greece).

**Methods** We used standard techniques for linear and nonlinear regression in order to check several models of the SAR, and stepwise multiple regression to check for the effects of factors other than area on species richness ('habitat diversity', elevation, and distance from nearest large island), as well as the performance of the Choros model. We also checked for the SAR of certain taxonomic and ecological plant groups that are of special importance in eastern Mediterranean islands, such as halophytes, therophytes, Leguminosae and Gramineae. We used one-way ANOVA to check for differences in richness between grazed and non-grazed islands, and we explored possible effects of nesting seabirds on the islands' flora.

**Results** Area explained a small percentage of total species richness variance in all cases. The linearized power model of the SAR provided the best fit for the total species list and several subgroups of species, while the semi-log model provided better fits for grazed islands, grasses and therophytes. None of the nonlinear models explained more variance. The slope of the SAR was very high, mainly due to the contribution of non-grazed islands. No significant SIE could be detected. The Choros model explained more variance than all SARs, although a large amount of variance of species richness still remained unexplained. Elevation was found to be the only important factor, other than area, to influence species richness. Habitat diversity did not seem important, although there were serious methodological problems in properly defining it, especially for plants. Grazing was an important factor influencing the flora of small islands. Grazed islands were richer than non-grazed, but the response of their species richness to area was particularly low, indicating decreased floral heterogeneity among islands. We did not detect any important effects of the presence of nesting seabird colonies.

**Main conclusions** Species richness on small islands may behave idiosyncratically, but this does not always lead to a typical SIE. Plants of Aegean islets conform to the classical Arrhenius model of the SAR, a result mainly due to the contribution of non-grazed islands. At the same time, the factors examined explain a small portion of total variance in species richness, indicating the possible contribution of other, non-standard factors, or even of stochastic effects. The proper definition of habitat diversity as pertaining to the taxon examined in each case is a recurrent problem in such studies. Nevertheless, the combined effect of area and a proxy for environmental heterogeneity is once again superior to area alone in explaining species richness.

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## Keywords

Aegean archipelago, Arrhenius model, Choros model, diversity, habitat types, island biogeography, plants, Small Island Effect, species–area relationship.

## INTRODUCTION

The terrestrial biota of small islands are considered by biogeographers and ecologists as extremely useful natural experiments, because they are relatively simple, well defined and, at the same time, abundant. Within the paradigm of the theory of island biogeography (MacArthur & Wilson, 1967), small islands have been given a special status because they are expected to deviate from the common pattern of the species–area relationship (SAR) due to their susceptibility to stochastic phenomena. The form of the SAR, i.e. the model that best describes it, especially when small islands (or small areas in general) are concerned, has been much disputed in the literature. According to various authors (e.g. He & Legendre, 1996; Rosenzweig & Ziv, 1999), at small geographical scales the semi-log model ( $S = k + b \log A$ , where  $S$  is the number of species,  $A$  is area, and  $k$  and  $b$  are parameters of the model) proposed by Gleason (1922) usually behaves better, while the power model (in its linearized form:  $\log S = c + z \log A$ ) of Arrhenius (1921) usually fits better across intermediate scales. According to He & Legendre (1996), for larger islands the best model should be the somewhat neglected logistic model proposed by Archibald (1949). In the search for the best mathematical description of the SAR, a variety of models, linear and nonlinear, have been proposed (see review by Scheiner, 2003; Tjørve, 2003). The general idea is that the species–area curve should be sigmoid, with the left part reflecting the atypical ‘behaviour’ of small islands.

This atypical behaviour, namely the well-known and much disputed Small Island Effect (SIE), refers to the absence of a significant effect of area on species richness below a certain island size threshold that varies between island groups, as well as between taxa (Whitehead & Jones, 1969; Lomolino & Weiser, 2001).

MacArthur & Wilson (1967) had suggested that turnover rates would be very high, leading to an independence of species richness from area on very small islands. Other factors, such as biotic interactions, stochastic events, habitat diversity, isolation and human impact, have been suggested as possible determinants of species diversity on small islands (Lomolino, 1994, 2000; Losos, 1996; Whittaker, 1998; Sadler, 1999; Schoener *et al.*, 2001; Triantis *et al.*, 2005).

Nevertheless, the crucial question of when an island is small enough to become a candidate for a SIE member cannot be answered in a straightforward way. One has to take into account the requirements of the organisms under study, in addition to the physiographic characteristics of the islands themselves. The lowest limit for many small-sized terrestrial organisms is more or less evident and is related to the minimum area where vegetation can be found, something

connected to the extent of the direct effects of waves for relatively long periods of time. The smallest possible viable area for terrestrial communities may vary to a certain degree, depending on the substrate, elevation, distance from the mainland or the nearest large island, local topography and location (e.g. islets in protected gulfs are not exposed to large waves), but within a small size-range. At the other extreme, the upper limits of ‘small’ island size are much vaguer, and their identification demands the use of a specific criterion, such as the identification of an inflection point in the species–area curve. One such method has been proposed by Lomolino & Weiser (2001).

Herein, we explore the patterns exhibited by plant species richness on 86 small islands of the Aegean Sea (Greece), in an attempt to identify possible effects of island size, elevation, habitat diversity, distance from species pool, nesting seabird colonies and grazing, the latter being the most important anthropogenic activity on such islands. We also explore the best fit model for the SAR, as well as the special patterns exhibited by certain important taxonomic and ecological subgroups of plant species. Because the data set consists exclusively of very small islands (all with a surface area smaller than 50 ha), should there be a SIE then we can expect not to find any systematic effect of area on species richness, at least for a subset containing the smallest of the islands.

There are many biogeographical studies of plants on small islands (e.g. Whitehead & Jones, 1969; Nilsson & Nilsson, 1978, 1982; Abbott & Black, 1980; Buckley, 1985; Woodroffe, 1986; Deshayé & Morisset, 1988; Höner & Greuter, 1988; Nilsson *et al.*, 1988; Rydin & Borgegård, 1988; Kohn & Walsh, 1994; Panitsa, 1997; Médail, 1998; Médail & Vidal, 1998; Hobohm, 2000; Khedr & Lovett-Doust, 2000; Ghazanfar *et al.*, 2001; Koh *et al.*, 2002; Morrison, 2002; Bergmeier & Dimopoulos, 2003; Pardo *et al.*, 2003). Among these, the works of Médail (1998), Médail & Vidal (1998), Khedr & Lovett-Doust (2000) and Bergmeier & Dimopoulos (2003) deal also with real (as opposed to ‘habitat’) Mediterranean islands. All the above mentioned authors either just present or explicitly address the SAR, while some discuss also the effects of habitat diversity and other factors on species richness. However, none of them addresses the SIE as such, even though many of these studies refer to small islands.

## METHODS

The data set used in this study consists of complete lists of plant species presence–absence data from 86 islets of the Aegean Sea (Greece) with an area smaller than (or equal to) 0.05 km<sup>2</sup> (50 ha). Data concerning geography and flora, as well as information about habitat types and plant communities,

are based on fieldwork by the authors (M.P. & D.T.) on all of the islets, between 1989 and 2005. The larger part of the data has been presented in Panitsa *et al.* (1994, 2003, 2004), Panitsa (1997), Panitsa & Tzanoudakis (1998, 2001) and Tzanoudakis *et al.* (1997), and have been complemented by some additional collections (M. Panitsa & D. Tzanoudakis, unpubl. data). The complete list of islets with their respective area, species richness, elevation, distance from nearest large island and an estimation of habitat diversity (see below) is presented in Table 1.

In order to test which SAR model fits better to our data, we applied the two common linear models ( $S/\log A$ ,  $\log S/\log A$ ), the more or less neglected logistic model of Archibald (1949), the convex Monod curve, the negative exponential, as well as the following sigmoid models: Logistic function, Gompertz model, Extreme value function, Lomolino function and the Cumulative Weibull distribution (for the description of these functions, see Tjørve, 2003).

The linear models were also tested separately for four subsets of the taxa, namely the halophytes, therophytes, leguminous taxa (family Leguminosae) and grasses (family Gramineae), and for four subsets of the islands (with and without grazing, with and without nesting seabird colonies). The four subsets of plant taxa are of special importance for small islands of the Mediterranean region. Halophytes, which are very well adapted to the extreme conditions prevailing, may dominate the smallest and/or lowest islets and are not affected by grazing. On larger islets, they dominate the sparsely vegetated littoral zone, which is directly affected by sea waves, and often the epilittoral zone, which is indirectly affected. Therophytes constitute a life-form category of annual plants which, depending on geographical and bioclimatological characteristics, is usually present in high percentages and very often dominates the other life forms of plants constituting the floras of Mediterranean islands and islets. However, it should be noted that therophytes are the prevailing growth form of plants capable of fast establishment in newly available areas all around the Mediterranean basin. As is well known, a high percentage of both therophytes and leguminous taxa in a flora is highly suggestive of disturbance in Mediterranean ecosystems (Höner, 1991; Panitsa *et al.*, 1994; Panitsa & Tzanoudakis, 1998). Leguminosae and Gramineae are among the richest and most characteristic families for these islands, with the former being also associated with anthropogenic effects, especially grazing. Nesting seabird colonies have been shown to be an important factor affecting plant communities on Mediterranean islands (Vidal *et al.*, 1998a,b, 2000) and elsewhere (e.g. Hogg & Morton, 1983). The seabird species nesting in colonies on the islands examined in this study are, in the main, the yellow-legged gull (*Larus cachinnans* Pallas, 1811) and, to a lesser extent, Audouin's gull (*L. audouinii* Payraudeau, 1826).

We also applied stepwise regression on total richness and the partitions of the data set mentioned above, using area, altitude, shortest distance from the nearest large inhabited island and habitat diversity as predictor variables. Habitat diversity was measured as the number of plant communities present on each islet, according to the definitions used in

Annex I of the Directive 92/43/EEC for the Natura 2000 Network, which also incorporate some physiographic attributes. Using more precise terminology (see Looijen, 1998), such a description corresponds to a measure of environmental heterogeneity, but biogeographers and community ecologists have extensively used similar metrics under the term 'habitat diversity'. It is not always clear which measure of geographical isolation to use, i.e. distance from the mainland, the nearest large island, or just the nearest island, and usually a different measure might be necessary for different islands (see for example Turchi *et al.*, 1995; Sfenthourakis, 1996; Morand, 2000; Brose, 2003). In the present case, we chose distance from the nearest large inhabited island because these islands are the most likely candidates for serving as species pools for the small islets examined here. We ran the regressions using both logarithmic and arithmetic values for all variables and we chose the best functions according to the behaviour of residuals and the total variance explained ( $R^2$ ). The same analysis was also applied separately on the aforementioned four groups of plants, as well as on the two subsets of islands, namely grazed and non-grazed. It was not possible to make a further distinction according to the intensity of grazing because even a very small number of grazing animals can have a critical effect on the flora of such small islands.

All regressions and the estimations of parameters were carried out with Statistica 6 (StatSoft, Inc., 2001). To minimize possible confounding effects due to high collinearity between independent variables in the stepwise regressions, we calculated tolerance and the variance inflation factor (VIF). In all cases, both for the logarithmic and the arithmetic values, tolerance was higher than 0.40, with a common cut-off threshold of 0.10, and the VIF values were lower than 4. Thus, multicollinearity was not a concern, and all independent variables were included in the regression (for further discussion, see Hair *et al.*, 1998).

The approximation to habitat diversity mentioned above was used also in the test of the performance of the Choros model (Triantis *et al.*, 2003, 2005), according to which species richness is fitted by the function:

$$\log S = m + k \log K,$$

where  $K$  is the product of the multiplication of area with habitat diversity. We also used one-way ANOVA to test for differences in species richness for the various data set partitions between grazed and non-grazed islands, and islands with and without nesting seabird colonies.

The presence of a significant SIE was tested using the method of Lomolino & Weiser (2001). These authors used simple linear regression with a breakpoint transformation to estimate the upper limit of SIE. The breakpoint, or piecewise regression model with two pieces, used, is:

$$Y = b_0 + b_1 \{ [\log_{10}(A) - T_1] \times [\log_{10}(A) \geq T_1] \}$$

where  $Y$  denotes the species richness ( $S$ ) or  $\log_{10}(S)$  for semi-log and log-log versions of the model, respectively,  $A$  the island

**Table 1** The complete list of the 86 small islands analysed, with their area (*A*, in km<sup>2</sup>), species richness (*S*), elevation (*E*, in metres), distance from nearest large island (*D*, in km), number of habitat types (*H*), application of grazing (N = no, Y = yes), number of therophytes (Th), halophytes (Ha), Leguminosae (Le), Gramineae (Gr), presence of nesting gull colonies (N = no, Y = yes), as well as their geographical coordinates

Island name	<i>A</i>	<i>S</i>	<i>E</i>	<i>D</i>	<i>H</i>	Grazing	Th	Ha	Le	Gr	Gulls	Longitude	Latitude
Ag. Kyriaki	0.150	59	76	1.3	3	Y	26	9	3	5	N	26°52'45"	37°09'50"
Ag. Nikolaos	0.119	69	30	0.4	3	Y	50	4	0	0	N	26°58'17"	37°47'45"
Antidragonera	0.150	89	40	0.6	3	Y	55	13	6	13	Y	23°06'50"	36°14'15"
Archontonisi	0.028	11	15	0.2	1	Y	4	1	1	1	N	26°15'48"	38°30'30"
Arefousa	0.175	43	65	0.7	3	Y	28	8	4	2	N	26°42'48"	37°20'01"
Aspronisi (east)	0.007	11	15	2.1	2	N	5	5	2	0	Y	26°48'10"	37°19'00"
Aspronisi (east_1)	0.037	34	30	1.4	2	N	16	9	4	3	Y	26°48'28"	37°18'26"
Aspronisi (north)	0.056	45	30	1.8	2	Y	18	5	2	7	Y	26°48'19"	37°19'04"
Aspronisi (northwest)	0.048	46	25	1.1	2	N	30	8	2	3	Y	26°48'11"	37°18'31"
Aspronisi (west)	0.010	7	15	1.9	2	N	4	1	0	0	Y	26°47'50"	37°19'04"
Diabates (east)	0.067	50	5	0.04	1	Y	36	4	4	8	Y	25°02'42"	39°51'24"
Diabates (west)	0.067	16	5	0.06	1	Y	10	3	0	3	Y	25°02'31"	39°51'26"
East Gourna	0.008	33	10	0.5	1	N	8	7	1	5	N	26°48'10"	37°09'50"
Faradonisi (northwest)	0.040	33	10	1.3	2	N	9	13	1	4	Y	26°45'50"	37°11'55"
Faradonisi (south)	0.025	22	5	0.7	1	N	9	9	1	4	Y	26°45'40"	37°11'55"
Faradonisi (southwest)	0.020	19	10	0.9	1	N	8	8	2	3	Y	26°45'40"	37°11'50"
Faradonisi megalos	0.160	60	55	0.8	3	Y	32	6	5	6	Y	26°45'45"	37°11'53"
Fragkonisi	0.225	103	75	4	3	Y	72	9	12	16	N	26°43'10"	37°15'25"
Glaronisi (north)	0.030	57	15	0.7	2	Y	28	7	4	5	Y	26°52'55"	37°05'30"
Glaronisi (south)	0.090	73	28	1.3	3	Y	34	5	6	5	Y	26°53'00"	37°05'10"
Ilias	0.023	6	10	0.03	1	Y	4	1	0	1	N	25°04'17"	39°50'11"
Imia (east)	0.017	17	20	10.2	2	Y	11	7	1	6	Y	27°08'50"	37°02'30"
Imia (west)	0.020	20	15	9.8	2	Y	15	6	3	3	Y	27°09'05"	37°02'10"
Kalapodi megalos	0.039	55	25	3.2	3	Y	32	14	3	8	Y	26°48'47"	37°15'23"
Kalapodi mikro	0.005	12	5	3.1	1	N	7	4	1	2	Y	26°48'15"	37°15'20"
Kalovolos	0.307	68	66	1.6	3	Y	42	2	7	4	N	26°46'01"	37°21'23"
Kapelo	0.009	1	10	4	1	N	0	1	0	0	N	23°05'40"	36°07'15"
Kapparonisi	0.068	57	18	1.8	3	Y	33	10	8	13	N	26°44'50"	37°16'15"
Katsaganaki	0.002	16	10	0.1	1	N	5	5	1	1	Y	27°00'05"	37°28'00"
Katsagani	0.090	72	30	0.2	2	Y	56	6	5	18	N	27°00'26"	37°28'03"
Kombi	0.090	68	20	0.4	1	Y	34	5	12	7	Y	25°14'07"	39°47'48"
Kommeno nisi	0.028	34	10	1.2	1	N	12	6	7	6	N	26°43'00"	37°20'30"
Koukonisi	0.472	11	10	0.2	2	Y	3	3	0	1	N	25°16'02"	39°53'06"
Kouloura_1	0.078	76	20	0.7	2	Y	43	5	10	8	N	26°47'57"	37°17'04"
Kouloura_2	0.020	45	30	0.2	2	N	23	7	4	4	N	26°47'35"	37°17'03"
Koumaro	0.100	37	20	0.1	2	Y	13	7	3	3	N	26°43'20"	37°24'05"
Kounelonisi	0.230	59	50	1.7	3	Y	39	10	2	4	N	26°58'46"	37°25'46"
Lidia	0.035	15	27	0.8	1	Y	6	6	1	1	N	22°54'05"	36°11'35"
Lyra	0.050	55	40	0.2	3	Y	41	6	6	9	N	26°46'00"	37°16'50"
Makronisi	0.034	15	30	0.4	3	Y	4	4	0	0	N	26°59'56"	37°48'01"
Makronisi_1	0.261	76	40	0.4	3	Y	60	8	8	10	N	26°45'15"	37°21'44"
Makronisi_2	0.197	58	30	2.1	3	Y	36	8	8	5	N	26°44'11"	37°16'28"
Marathi	0.355	90	51	0.6	3	Y	75	5	16	14	N	26°43'35"	37°22'12"
Mavra (east)	0.148	38	20	40.6	2	N	19	10	3	3	Y	26°22'52"	36°59'48"
Mavra (west)	0.132	32	20	41.4	2	N	13	9	2	3	Y	26°22'06"	36°59'43"
Megali Dragonera	0.320	109	36	0.6	3	Y	71	10	6	13	Y	23°06'45"	36°13'20"
Megalo Stroggylo	0.030	12	29	1.2	1	Y	5	5	1	2	N	22°54'40"	36°10'30"
Megalo Trachili	0.225	11	5	0.2	2	Y	5	3	0	2	N	25°13'48"	39°53'00"
Mikro Trachili	0.135	6	5	0.1	1	Y	2	3	0	0	N	25°13'25"	39°52'59"
Minaronisi	0.021	45	20	0.4	2	Y	21	6	2	4	Y	26°44'36"	37°21'32"
Neronisi	0.500	27	63	0.2	3	Y	18	5	2	2	N	26°59'30"	37°28'30"
Nisida Manoli	0.029	55	30	1	2	Y	26	5	7	4	Y	26°43'44"	37°20'19"
Paplomata	0.004	26	3	0.1	1	N	10	4	1	2	N	26°46'50"	37°18'30"
Patelidi	0.025	8	5	0.7	1	N	3	4	1	0	N	26°47'30"	37°12'40"

Table 1 continued

Island name	A	S	E	D	H	Grazing	Th	Ha	Le	Gr	Gulls	Longitude	Latitude
Piatio	0.060	56	20	1.8	1	Y	26	7	5	8	N	26°44'40"	37°16'40"
Piganousa	0.350	101	139	0.7	3	Y	56	6	8	6	N	26°54'00"	37°07'50"
Pitta	0.024	22	20	8	2	N	11	7	3	3	Y	27°04'00"	37°05'10"
Plakousa	0.050	17	10	0.6	2	N	9	9	0	1	Y	26°49'00"	37°12'10"
Plochoros	0.067	60	20	0.7	2	Y	42	7	16	7	N	26°45'30"	37°16'06"
Pontikos	0.103	18	30	0.8	3	Y	5	4	2	2	N	26°16'30"	38°30'25"
Prassonisi	0.013	14	10	1	1	N	1	1	0	0	N	26°57'47"	37°47'51"
Prassonisi_3	0.040	15	13	0.2	1	N	6	7	1	4	N	23°05'55"	36°16'00"
Prassonisi_1	0.011	13	2	1.3	1	N	4	8	0	3	N	26°59'29"	37°29'01"
Prassonisi_2	0.012	32	15	8	1	N	16	7	2	5	Y	27°04'55"	37°03'15"
Prassou	0.500	97	40	8	4	Y	57	12	13	12	N	23°14'50"	35°58'30"
Psathi	0.052	67	20	1.5	2	Y	46	9	5	13	Y	26°45'27"	37°21'06"
Psathonisi	0.127	44	10	0.7	2	Y	26	6	3	9	Y	26°57'10"	37°29'06"
Psonos	0.071	93	30	1.3	2	Y	57	6	8	15	N	26°45'08"	37°16'03"
Saraki	0.007	16	30	7.8	1	N	8	6	0	3	Y	26°42'40"	37°14'00"
Spartonisi	0.025	39	15	1.3	2	Y	19	8	7	7	Y	26°43'12"	37°20'21"
Stroggyli	0.096	62	20	1.1	2	Y	42	5	1	9	N	26°58'50"	37°29'12"
Stroggyli_1	0.207	67	91	1.1	2	Y	51	8	7	7	N	26°43'02"	37°22'25"
Stroggyli_2	0.150	44	76	0.5	3	Y	26	1	2	3	N	26°48'45"	37°12'50"
Thimonies	0.010	8	10	0.1	1	N	1	4	0	4	N	23°18'20"	35°53'40"
Tiganaki	0.042	55	20	0.1	1	Y	44	4	8	7	N	26°44'55"	37°22'00"
Tigani	0.140	12	5	0.03	1	Y	6	2	0	6	N	25°02'44"	39°49'48"
Trypiti megali	0.072	72	30	1	2	Y	29	14	4	8	Y	26°48'55"	37°12'55"
Trypiti mikri	0.020	44	15	0.8	1	N	13	9	4	3	Y	26°48'55"	37°12'50"
Vatopoula	0.007	54	15	2.4	1	N	20	7	6	10	N	26°16'42"	38°29'23"
Vatos	0.386	93	30	2.6	3	Y	47	8	9	10	Y	26°17'10"	38°29'23"
Velona	0.070	63	15	0.3	3	Y	40	6	4	8	N	26°53'20"	37°05'50"
West Gourna	0.006	7	8	0.5	1	N	4	5	0	1	N	26°48'15"	37°09'50"
Zouka (Megali)	0.028	86	20	0.4	1	Y	61	8	5	11	N	26°45'00"	37°21'36"
Zouka (Mikri)	0.008	79	15	0.2	1	Y	40	8	5	11	N	26°44'50"	37°21'37"
(unnamed_1)	0.005	12	10	1.2	1	N	5	3	0	0	Y	26°45'15"	37°16'15"
(unnamed_2)	0.0005	1	2	1.7	2	N	0	1	0	0	N	26°45'00"	37°16'50"

area,  $T_1$  the upper limit of the SIE, and  $[\log_{10}(A) \geq T_1]$  a logical variable that returns the value of 0 or 1 when false or true, respectively, while  $b_0$  is the intercept, denoting a measure of the species richness on small islands, and  $b_1$  is the slope of the breakpoint regression. From this model, one can calculate  $T_1$ , which is the area below which all islands are subject to a SIE.

## RESULTS

The best fit linear SAR curve for total plant richness is the one provided by the linearized Arrhenius model (log-log), which explained 32.3% of total variance (see Table 2 for the results of all SAR models). All sigmoid models tested were statistically significant ( $P < 0.05$ ), but explained slightly less than 32% of total variance, but since they contain more parameters, even this small difference is adequate for not preferring them. Also, all convex models had similarly smaller explanatory power. Among the linear models, the semi-log model ( $S - \log A$ ) fitted better to grazed islands, grasses and therophytes, whereas the log-log model was again better for non-grazed, halophytes, leguminous taxa, and islands with and without gull nests (Table 3). The SAR

for halophytes had a very low  $R^2$ . In general, area explained a rather small percentage of total variance in species richness for all groups (according to  $R^2$ ). Finally, the Choros model had a better fit to the data, even though the percentage of total variance explained remained small (Table 2).

As can be seen in Table 3, the slope of the SAR is large (0.40), and it is still larger when only non-grazed islets are considered (0.45). The slope for grazed islets in the log-log model is much lower (0.19), although this model is not statistically significant. The log-log SARs for all data set partitions are shown in Fig. 1.

The method of Lomolino & Weiser (2001) for the detection of a significant SIE, when applied to the logarithmically transformed data, resulted in a  $T_1 = 0.00051$ , which means that a SIE is not detectable. The same model, when applied to  $S/\log A$  values, resulted in a  $T_1 = 0.01$ , thus including 14 islands ( $R^2 = 0.315$ ). Nevertheless, this value is not different from the  $R^2$  value offered by the linear  $S/\log A$  model, while the  $S/\log A$  model does not provide a better description of the SAR. Therefore, we can assume that no significant SIE is present in this data set.

**Table 2** Statistically significant SAR functions (at the 0.05 *P*-level) according to a variety of models tested for the plants of 86 small Aegean islands. The last row shows the Choros model (Triantis *et al.*, 2003) for the same data set. The documentation of all other models can be found in Tjørve (2003) and in Archibald (1949). *S* is the number of taxa, *A* is area, and *K* is the product of area and habitat diversity

Model	Function	<i>R</i> <sup>2</sup>
log-log	$\log S = 2.02 + 0.40 \log A$	0.323
<i>S</i> -log <i>A</i>	$S = 78.38 + 26.73 \log A$	0.312
Monod	$S = 68.73[A/(0.02 + A)]$	0.310
Negative exponential	$S = 59.79[1 - \exp(-31.67A)]$	0.293
Logistic (Archibald)	$S = 558.18/(6.39 + A^{-0.63})$	0.319
Logistic function	$S = 59.72/[1 + \exp(-46.50A + 1.09)]$	0.312
Gompertz	$S = 60.87 \exp[-\exp(-31.15A + 0.36)]$	0.311
Extreme value function	$S = 69.39\{1 - \exp[-\exp(8.42A - 0.68)]\}$	0.274
Lomolino	$S = 87.35/1 + 4.23 \log^{(0.05/A)}$	0.319
Cumulative Weibull	$S = 72.60[1 - \exp(-4.45A^{0.53})]$	0.319
Choros	$\log S = 1.85 + 0.33 \log K$	0.353

**Table 3** Best fit linear models for the complete data set and certain partitions of islands (grazed/non-grazed, with/without nesting gulls) and plant taxa. Symbols as in Table 2

	Best linear model	<i>R</i> <sup>2</sup> -value	<i>P</i> -value	<i>z</i> -value	Intercept
All species	log <i>S</i> -log <i>A</i>	0.32	< 0.001	0.40	2.02
Grazed	<i>S</i> -log <i>A</i>	0.11	< 0.02	21.69	74.50
Non-grazed	log <i>S</i> -log <i>A</i>	0.31	< 0.001	0.45	2.06
Therophytes	<i>S</i> -log <i>A</i>	0.33	< 0.001	19.16	49.81
Halophytes	log <i>S</i> -log <i>A</i>	0.06	< 0.02	0.12	0.89
Leguminosae	log <i>S</i> -log <i>A</i>	0.25	< 0.001	0.33	0.96
Gramineae	<i>S</i> -log <i>A</i>	0.15	< 0.001	2.74	9.09
With gulls	log <i>S</i> -log <i>A</i>	0.57	< 0.001	0.44	2.16
Without gulls	log <i>S</i> -log <i>A</i>	0.28	< 0.001	0.41	1.97

According to the stepwise regressions (Table 4), only area and altitude affect species richness. These two variables are positively correlated but with a quite low correlation coefficient ( $R^2 = 0.352$ ). When the same analyses are applied separately for grazed and non-grazed islands, altitude is the only significant parameter entering the model for grazed islands, and area the only one for non-grazed. Environmental heterogeneity ('habitat diversity') and distance from nearest large island do not affect total species richness in any case. Area and altitude are the only variables that enter the model also for therophytes, while area alone counts for grasses and legume species richness. For halophytes, besides area, isolation also enters the model. Area, elevation and isolation explain a high percentage (72%) of total variance for islands with nesting gull colonies, while only elevation enters the model for those without gull colonies. It should be noted, that in most cases the percentage of total variance explained by the best model is small (< 45%).

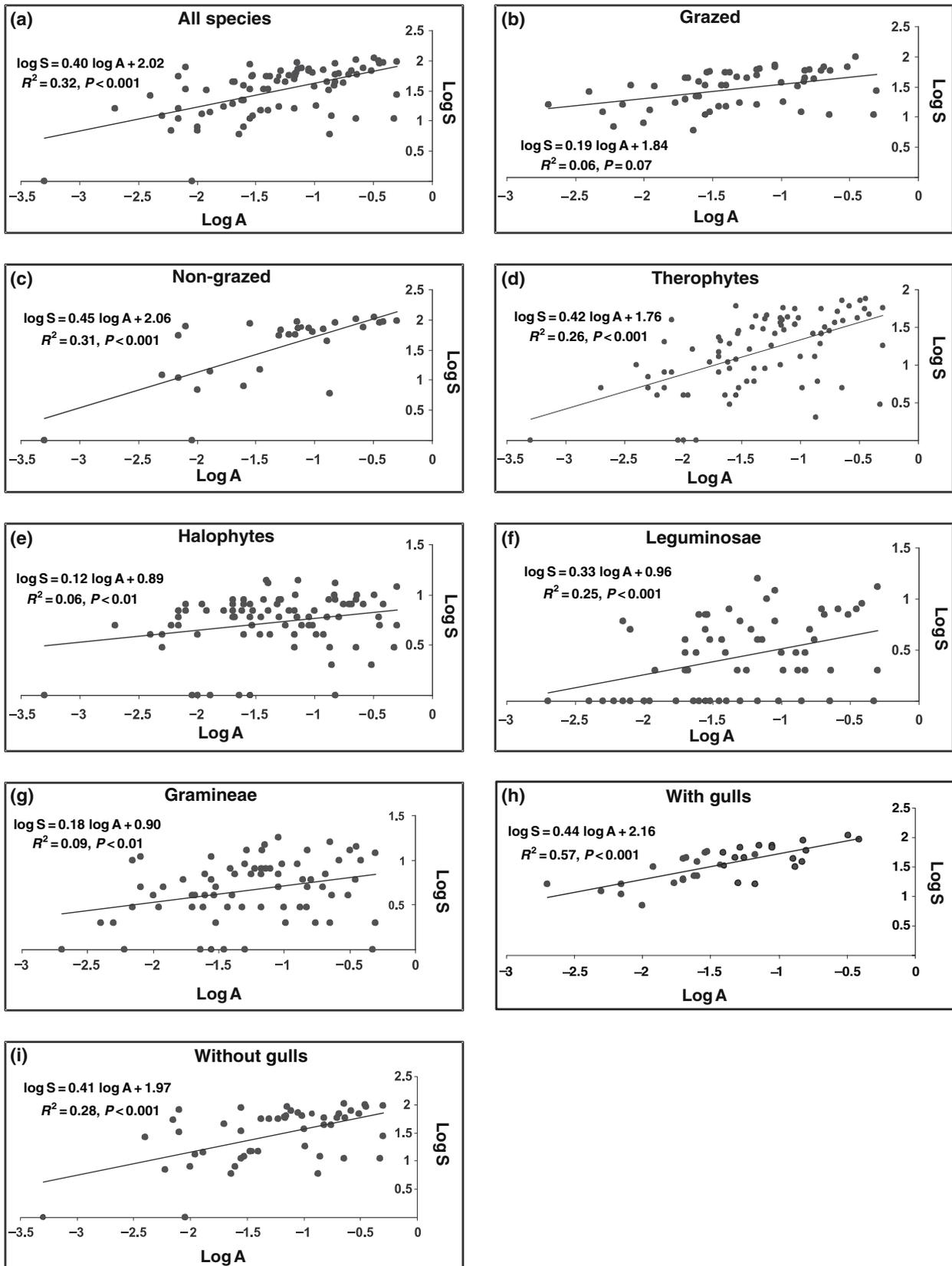
Grazed islands have richer total plant communities (Table 5), and the same holds also for therophytes, grasses and leguminous taxa, whereas the richness of halophytes does not differ between grazed and non-grazed islands. The presence of nesting gulls (Table 6) does not seem to be related to grazing, and only halophytes seem to be richer on islands with nesting gull colonies (leguminous taxa show the opposite trend but at a marginally significant level).

## DISCUSSION

The plant communities of small Aegean islands conform fairly well to the traditional linearized power model for the SAR, and no apparent SIE can be detected. Nevertheless, the method we used here has certain methodological problems (see Gentile & Argano, 2005), but it is the only one available so far for the detection of the SIE. The only factor, besides area, that seems to affect plant species richness is the maximum elevation of islets. This result is in agreement with several other studies of plants on small islands (Buckley, 1985; Rydin & Borggård, 1988; Khedr & Lovett-Doust, 2000), but it is in contrast to Kohn & Walsh (1994) and Médail & Vidal (1998), who found a significant contribution attributable to habitat diversity. Nevertheless, Kohn & Walsh (1994) did not check for the effects of elevation, and they identified area as the most important variable using path analysis. At the same time, Médail & Vidal (1998) did not separate the effects of habitat diversity and area, while they also found that elevation had a significant effect. Elevation can be perceived as representing both area (since in small islands the actual land surface area enlarges to a significant degree with elevation) and elements of habitat diversity (higher elevation usually means a more complex topography, a wider variety of micro-habitats, and a reduced influence of the sea; Schoener *et al.*, 2001). The fact that area alone predicts richness of non-grazed islands, whereas elevation alone predicts richness of grazed ones, indicates that the combined effect of area and altitude on total richness results from the separate effects of these parameters on different partitions of the island list.

The finding that halophyte richness is positively associated with distance from the nearest species pool may be related to the increased representation of habitats with extreme conditions (constant salt pressure) in which halophytes thrive, but which other plants cannot tolerate, on more distant islets. Distant islets are usually less protected and more exposed to the effects of seawater, thus sustaining more halophytes. These factors may enable halophytes to dominate the plant communities of distant islets (Panitsa, 1997), also taking the fact into account that halophytes are not affected by grazing (see Table 5). There is no straightforward interpretation of the results for species richness on islands with and without nesting gull colonies. Further work is needed to clarify the interplay among the various factors involved.

The slope of the regression line is quite large, but similar values have been found in several other studies of plants on small islets. For example, the slope of the log-log model for



**Figure 1** Log-log SARs for the various partitions of plant species and islands analysed in the present paper. The unit of area is  $\log \text{km}^2$ .

Taxa	Function	Adjusted $R^2$	$P$ -value
All species	$\log S = 1.11 + 0.21 \log A + 0.51 \log E$	0.44	< 0.001
All species (grazed islands)	$\log S = 0.86 + 0.56 \log E$	0.29	< 0.001
All species (non-grazed islands)	$\log S = 2.06 + 0.45 \log A$	0.28	< 0.002
Therophytes	$S = 9.57 + 10.76 \log A + 22.98 \log E$	0.43	< 0.001
Halophytes	$\log S = 0.90 + 0.12 \log A + 0.14 \log D$	0.14	< 0.001
Leguminosae	$\log S = 0.96 + 0.33 \log A$	0.24	< 0.001
Gramineae	$S = 9.09 + 2.74 \log A$	0.14	< 0.001
All species (with gulls)	$\log S = 1.81 + 0.37 \log A + 0.35 \log E - 0.16 \log D$	0.72	< 0.001
All species (without gulls)	$\log S = 0.48 + 0.76 \log E$	0.43	< 0.001

**Table 4** Stepwise linear regressions for the complete data set and its partitions. Only variables that enter the model are shown, with the total variance explained and the statistical significance of the respective model.  $E$  stands for elevation,  $D$  for shorter distance from nearest mainland or large island. Other symbols as in previous tables

**Table 5** The comparison of species richness between grazed (GR) and non-grazed (NG) islands for the complete data set and certain partitions of taxa

Plant groups	ANOVA	Average values
All species	$F = 37.25$ ( $P < 0.001$ )	GR = 53.6, NG = 22.4
Therophytes	$F = 37.59$ ( $P < 0.001$ )	GR = 32.3, NG = 9.3
Halophytes	$F = 0.06$ n.s.	GR = 6.3, NG = 6.1
Leguminosae	$F = 18.12$ ( $P < 0.001$ )	GR = 5, NG = 1.7
Gramineae	$F = 23.14$ ( $P < 0.001$ )	GR = 6.9, NG = 2.7
With gulls	$F = 23.37$ ( $P < 0.001$ )	GR = 56.5, NG = 24.3
Without gulls	$F = 13.43$ ( $P < 0.001$ )	GR = 52.1, NG = 19.9

**Table 6** The comparison of species richness between islands with nesting gull colonies (GN) and islets without gull nests (NN) for the complete data set and certain partitions of taxa

Plant groups	ANOVA	Average values
All species	$F = 0.15$ n.s.	GN = 41.3, NN = 43.8
Therophytes	$F = 1.74$ n.s.	GN = 21.6, NN = 27.3
Halophytes	$F = 8.64$ ( $P < 0.005$ )	GN = 7.3, NN = 5.5
Leguminosae	$F = 3.89$ ( $P = 0.05$ )	GN = 3.8, NN = 5.5
Gramineae	$F = 0.87$ n.s.	GN = 5.5, NN = 6.3
Grazed	$F = 0.30$ n.s.	GN = 56.5, NN = 52.1
Non Grazed	$F = 0.68$ n.s.	GN = 24.3, NN = 19.9

islands with an area smaller than 50 ha in the data of Médail & Vidal (1998) is 0.46, Rydin & Borgegård (1988) report values varying between 0.36 and 0.56 during the 20th century for very small islets in Lake Hjälmaren, and Fridley *et al.* (2005) report a similarly high rate of plant species accumulation across very fine geographical scales. This behaviour of slopes for very small areas can also be seen in other groups. Rusterholz & Howe (1979), for example, report a slope of 0.44 for the birds on small islands in a Minnesota lake (see also Rosenzweig, 1995). Nevertheless, examples of smaller slopes for small islets are not uncommon (e.g. Hobohm, 2000; Pardo *et al.*, 2003). As Williamson *et al.* (2001, 2002) pointed out, the left hand side

of the species–area relationship does not exhibit a steady behaviour. In some cases, the relationship flattens out and in others it becomes steep or follows the linearity of the larger islands.

The application of grazing, usually by goats and sometimes also by sheep, is a common practice on small islands of the Aegean, but in several cases the local conditions do not permit it (e.g. where the coasts are very steep, if the islands are very distant, if they are covered mainly by halophytic vegetation, or when they are of special status regarding ownership). According to Snogerup & Snogerup (2004), goats and sometimes sheep are transported annually by boat to the grazed islets and this causes the introduction of plants through diaspores attached to wool and contained in faeces of the animals, or dropped by the persons transporting them. Many of these plants are weeds, others common species of the neighbouring large islands from where the animals were taken. An introduced species that does not, or rarely, reaches the islets with natural dispersal agents has to withstand two tests. First, it must establish mature individuals against the competition from existing species, which is rather difficult (although it may get some help in the form of open spaces created by the grazing animals), and then for several generations it has to withstand the more-or-less extreme conditions of the islet. Höner (1991) made a series of 110 introductions with 30 species on ungrazed small offshore islets around Karpathos, which already had an established plant-cover, using various amounts of seeds, fruits and bulbs. This experiment resulted in only 18 cases of plants persisting for the first year, and in only one species persisting after 6 years and able to reproduce. However, Snogerup & Snogerup (2004) have classed 100 taxa as probably introduced by grazing animals into one or a few islets, 45 of which were still present after 10 years on one, or rarely two, islets. According to Panitsa (1997) and Panitsa & Tzanoudakis (1997), who presented significant differences concerning the floristic composition of 24 islets within a 20 year period, the flora of small islands is not constant, but rather is in a very dynamic state. It is well known that islets are very fragile ecosystems on which random factors, intense environmental

fluctuations (storms, wave action, etc.) or human interference of even a low intensity can affect the flora and vegetation to a great extent, mainly because of the small plant population size. Thus, as a general pattern, grazing leads to a strikingly different vegetation structure, whereas the small ungrazed islands are one of the very few ecosystem types in the Mediterranean almost without human interference (Bergmeier & Dimopoulos, 2003). Consequently, the flora of ungrazed islands should have had more time than grazed ones for relaxation and to reach an equilibrium state. Their elevated slope, then, should reflect processes that are inherent in such small islet biota. The poorer flora of non-grazed islets corresponds to their 'normal' condition, whereas grazing permits the establishment of more species. These species, however, are more or less the same in all cases, hence the non-conformity to the log-log model and the poor fit of the SAR. Also, the fact that non-grazed islets conform better to the log-log model and that no SIE is present can be regarded as evidence that the processes involved in the structuring of Aegean small island plant communities are not particularly stochastic.

An important factor affecting the flora of small islets is the presence of seabird colonies. Their impact on islet floras is correlated with gull density, and consists of physical and chemical disturbance, as well as the alteration of competitive processes (Vidal *et al.*, 1998a). According to Vidal *et al.* (1998b), gull colonies on Riou archipelago (France) have important consequences on habitat heterogeneity and diversity on small islets (< 3 ha) compared to larger ones because sea birds are the cause of significant deposition of guano and nest material, which often permits the establishment of permanent vegetation cover on unvegetated rocky zones and cobble shores. By contrast, the original habitat diversity and the presence of disturbed areas on the largest islands mitigate the impact of perturbations caused by seabirds. Snogerup & Snogerup (1987, 2004), in the framework of their repeated floristic observations on Aegean islets, found that gulls disperse plants that are already common in these environments and so act as a natural, and certainly very old, dispersal agent on the islets. They confirmed that the yellow-legged gull, which breeds on several of the islets and frequently visits all of them, regularly deposit considerable numbers of the large *Pistacia lentiscus* seeds, which have in several cases been found germinated, and also can disperse several other species such as *Rumex pulcher* and *Olea europaea*. In our case, however, only halophytes seem to be positively affected by the presence of nesting gull colonies. The relatively small total number of halophytes and the small difference between mean halophyte richness between islands with and without gulls did not allow for a discernible effect on total species richness. We should also note that gulls may not nest every year on the same islands, so they may have affected, in a comparable manner, more islands than those identified here. Thus, it is possible that islet species richness is uniformly affected by gulls, so that no obvious effect can be detected in comparisons among partitions of the data set. The interaction of plant communities with gulls should be investigated further, mainly at the level of community structure.

It is worth mentioning that floristic diversity between islets seems to be higher for the smaller ones. Sorensen's coefficient yielded values not higher than 0.5 (0.02–0.5) between the islet floras, but also between each islet and the larger neighbouring inhabited island (Panitsa, 1997). Even plant taxa that seem to be well adapted to such small islet ecosystems ('islet specialists') show an uneven distribution in the area studied (Panitsa & Tzanoudakis, 2001). Similar observations concerning small island phenomena have been reported by Runemark (1969), Snogerup (1985), Carlstrom (1987), Snogerup & Snogerup (1987, 2004), Höner (1991) and Höner & Greuter (1988).

At the same time, we could assume that, because of the relatively small size of the islands, their vegetation may have become dominated by plant species well-adapted for between-island dispersal, thus obscuring the effects of area and isolation. This is in accordance with Koh *et al.* (2002), who found that in their similar data set there is no significant correlation between species of vascular plants and any of the tested biogeographical variables.

In a similar study, Morrison (1997, 2002) concluded that the three variables commonly used in studies of determinants of insular species richness (total island area, distance and elevation) were relatively poor predictors of plant species richness on small islands in the Bahamas. He proposed that the predictive power of the models tended to be higher for groups of islands that were more sheltered by neighbouring islands. Exposed islands, although separated by relatively small distances from nearby protected islands, may be impacted by storms much more severely and so possess many fewer species.

The low percentage of explained variance by the variables used here is suggestive of a role for additional factors, which we did not address in this work. In any case, area seems to play a particularly important role, even though we should note that the way 'habitat diversity' has been defined may lead to an underestimation of its actual effects. Habitat diversity is often presumed to increase in direct relation to island area (Watson, 1964; Kohn & Walsh, 1994). If larger islands support greater habitat diversity, this increased habitat diversity might promote increased species richness (Kohn & Walsh, 1994; Ricklefs & Lovette, 1999). Moreover, island size can influence the presence of particular habitat types (e.g. Whitehead & Jones, 1969; Kohn & Walsh, 1994), thus it might indirectly affect the species number present on the island, particularly if a high proportion of the species involved are habitat specialists (Hart & Horwitz, 1991). In principle, habitat availability is one of the main factors influencing species diversity especially on small islands. Few species may find suitable habitats that allow them to establish on small islands (Whitehead & Jones, 1969; Triantis *et al.*, 2005). Nevertheless, the description of habitat diversity is quite difficult for plant species, for a detailed analysis should be based on information regarding many physico-chemical parameters of the soil, micro-climatic data, etc., all of which are hard to collect (in many instances, unrealistically so) and usually are not available in the context of extensive biogeographic studies. Also, many dimensions of plant habitat vary at a very fine geographical scale (e.g. soil pH

may vary within a few square metres), making their recording an almost impossible target, while others are almost invariable at the geographical scale usually addressed by such studies (e.g. rainfall and sunlight).

The approach to habitat diversity adopted in the present work leads to a somewhat cyclical, albeit inevitable, definition of habitat types (because the more species present, the more plant assemblages are likely to occur). Despite this partial circularity, stepwise regression could not identify habitat diversity as an important factor affecting plant species richness.

On the other hand, the better performance of the Choros model in the present study indicates that the involvement of a measure of habitat (more properly, environmental) heterogeneity in the species–area model leads to a more effective description of species richness than area alone. It should be noted, however, that caution is necessary in the use of proxy measures of habitat diversity because measures not informed by the natural history of the focal taxon can reduce the effectiveness of the model (see Triantis *et al.*, 2003, 2005). Further development of these models should focus on the assumptions underlying how species and ecologists perceive habitats.

From another perspective, taking a conservation-related point of view, this work corroborated previous findings that even traditional, low-intensity human practices, such as grazing by free-living goats and sheep, affect significantly the processes shaping plant communities on small islets, increasing total species richness but decreasing overall heterogeneity (beta diversity).

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