

# Biodiversity patterns of terrestrial isopods from two island groups in the Aegean Sea (Greece): Species–area relationship, small island effect, and nestedness<sup>1</sup>

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**Abstract:** Although almost one third of Aegean islands have an area smaller than 1 km<sup>2</sup>, very few studies have concentrated on this spatial scale. We investigate biodiversity patterns of terrestrial isopods in 2 island groups (Kalymnos and Astypalaia) of the Aegean Sea, consisting mainly of small islands and characterized by different geological histories, isolation, and species source pools. We focus on the species–area relationship (SPAR), community nestedness and the investigation of the small island effect (SIE) in these island groups. The slopes of the SPARs for terrestrial isopods of the 2 groups are almost identical and place the 2 island groups within the intraprovincial category. The SIE investigated was detected in both island groups, with the Kalymnos group exhibiting a higher upper limit (the island size threshold under which an increase of species number with increase of area in small islands is not observed). Both island groups are highly nested and exhibit similar levels of nestedness. Despite the different geological histories, isolation, and source pools, the 2 island groups exhibit great similarity in all the patterns investigated. The islands studied still “behave” as parts of a continuous land mass, with high numbers of species even on the smallest islands, limited net effects of island size, and a significant contribution of the interrelationship between area and environmental heterogeneity to the total species richness.

**Keywords:** Aegean Sea, environmental heterogeneity, small islands, species–area relationship, terrestrial isopods.

**Résumé :** Bien que presque un tiers des îles de la mer Égée soient plus petites que 1 km<sup>2</sup>, très peu d'études ont été réalisées à cette échelle spatiale. Nous examinons les patrons de biodiversité des isopodes terrestres dans 2 groupes d'îles de la mer Égée (Kalymnos et Astypalaia), consistant principalement en de petites îles caractérisées par des histoires géologiques, d'isolement et d'origines des espèces différentes. Nous nous concentrons sur la relation aire-espèce, l'emboîtement des communautés et l'étude de l'effet « petite île » dans ces groupes d'îles. Les pentes des relations aire-espèce pour les isopodes terrestres des 2 groupes d'îles sont presque identiques et placent ces 2 groupes d'îles dans la catégorie intraprovinciale. L'effet « petite île » a été détecté dans les 2 groupes d'îles, le groupe de Kalymnos démontrant une limite supérieure plus élevée (le seuil de taille d'île auquel une augmentation du nombre d'espèces n'est pas observée lors d'une augmentation de la taille de l'île). Les 2 groupes d'îles sont fortement emboîtés et démontrent des niveaux similaires d'emboîtement. Malgré des histoires géologiques, d'isolement et d'origines des espèces différentes, les 2 groupes d'îles démontrent une grande similitude dans tous les éléments examinés. Les îles étudiées se comportent encore comme si elles faisaient partie d'une masse continentale ininterrompue, avec des nombres d'espèces élevés même dans les îles les plus petites, des effets nets limités de la taille des îles et une contribution significative à la richesse totale en espèces de l'interrelation entre la taille et l'hétérogénéité environnementale.

**Mots-clés :** hétérogénéité environnementale, isopodes terrestres, mer Égée, petites îles, relation aire-espèce.

**Nomenclature:** Schmalzfuss, 2003.

## Introduction

The biogeography of the Aegean has attracted biogeographic interest for more than 40 y (see Watson, 1964) due to the complex geological history of the area, the high per-

centages of endemism, and the fact that it is the only area of the world with floral and faunal elements originating from 3 different geographical regions, namely Europe, Asia, and Africa. These features have led to a noteworthy increase in the number of studies addressing biodiversity patterns in the Aegean region during the last decade (see Sfenthourakis, 1996; Sfenthourakis, Giokas & Tzanatos, 2004; Hausdorf & Henning, 2005).

The Aegean archipelago consists of 7852 islands and islets. The vast majority of these (7439) do not exceed

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1 km<sup>2</sup> in area. Despite the fact that almost one third of Aegean islands have a total area ranging from 0.001 to 1 km<sup>2</sup>, very few studies have concentrated on this spatial scale. The majority of these studies are about plants (see Panitsa *et al.*, 2006 and references therein) and just a few refer to animals, mainly invertebrates (Botsaris, 1996; Triantis *et al.*, 2005; Triantis, 2006). Furthermore, the majority of biogeographic studies in the Aegean have concentrated at large spatial scales (*i.e.*, large parts of the Aegean, such as the Kyklades), while very few of them focus on well-defined local island groups (Mylonas, 1982; Sfenthourakis, 1996a,b; Dennis *et al.*, 2000; Fattorini, 2002; Simaiakis, Minelli & Mylonas, 2006).

As Lomolino and Weiser (2001) note, ecologists and biogeographers have a tendency to disproportionately sample large islands in contrast to the usually much more numerous small islands despite the insights that can be gained, especially regarding patterns such as the species–area relationship, the small island effect, and community nestedness. As far as invertebrates are concerned, the study of small islands is of prime interest, as they form the major faunistic element of these islands due, among other factors, to the smaller mean size of these organisms in comparison to vertebrates or plants.

Among the Crustacea, Oniscidea is undoubtedly the group that has been most successful in colonizing terrestrial environments. Even though these animals explore a variety of habitats, in general they are characterized by low

dispersal ability and a relatively high degree of stenoecy (Gentile & Argano, 2005). Oniscidea are also very sensitive to habitat heterogeneity. Recent studies of Oniscidea from Mediterranean islands have shown that the number of species is directly proportional to habitat heterogeneity, which may also influence community structure (Sfenthourakis, 1996a). As a result of these characteristics, Oniscidea are a valuable tool when investigating the evolutionary dynamics of insular biota and represent a good biological model for the study of colonization processes. In the present study we investigate biodiversity patterns of terrestrial isopods in 2 island groups of the Aegean Sea, consisting mainly of small islands and characterized by different geological histories. More specifically, we focus on the species–area relationship, community nestedness, and investigation of the small island effect (SIE) in these island groups.

### Methods

#### STUDY AREA

The island group of Astypalaia is one of the most isolated groups of the Aegean Sea, forming a transitional zone between Kyklades and Dodecanisos islands. The largest island is Astypalaia, with a total surface of 95.87 km<sup>2</sup> and an elevation reaching 482 m. Some 20 small islets are found within the 200-m isobath around Astypalaia, while Ofidousa lies outside this isobath (Figure 1). Data on the geological history of this island group are quite sparse, and no consensus has been reached on the time of isolation and

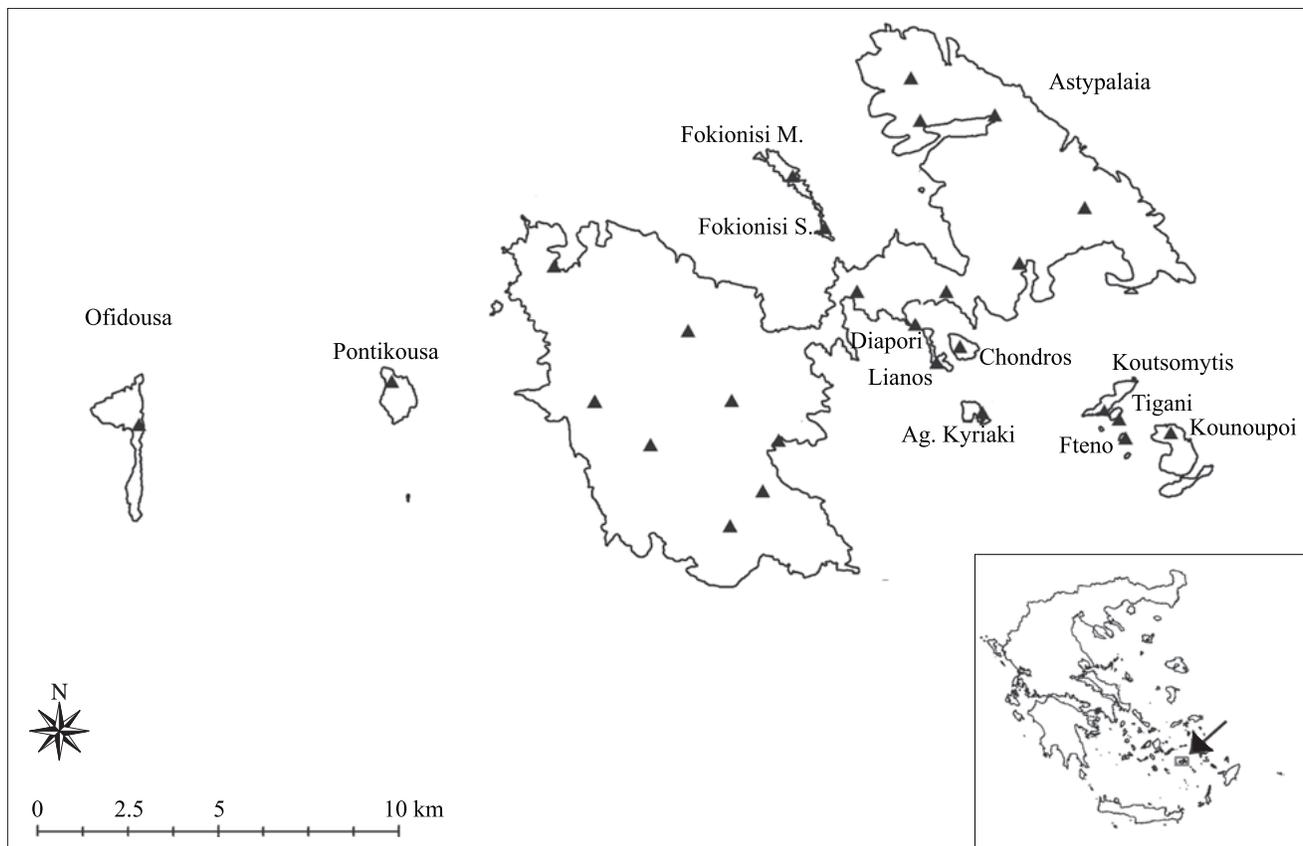


FIGURE 1. Map of the Astypalaia island group, its relative position in the Aegean, and the sampling stations (triangles).

the major geological events affecting the area (Dermitzakis, 1990; Lambeck, 1996). As far as the formation of the island group is concerned, Ofidousa and Pontikousa islets were isolated around 22 000 y (Perissoratis & Conispolatis, 2003) or 14 000 y (Lambeck, 1996) before present, and the rest of the islets were formed during the Holocene (Lambeck, 1996; Perissoratis & Conispolatis, 2003).

The island group of Kalymnos is situated in the eastern part of the Aegean Sea, between the islands of Leros and Kos (Figure 2). The main island of Kalymnos has a total area of 110 km<sup>2</sup>. The geomorphology of the island is complex, with a significant number of hills exceeding 300 m, Profitis Ilias being its highest peak (669 m). The second largest island of the group is Pserimos (14.6 km<sup>2</sup>), which is situated between Kalymnos and Kos. The formation of the group took place quite recently. The area was connected to Asia Minor at least until 21 000 y ago. Thereafter, around 11 000–9000 y ago, it was disconnected from the coast of Asia Minor but remained part of an elongated landmass that included the island of Leros and the island group of Arkoi (Lambeck, 1996; Perissoratis & Conispolatis, 2003). Hence, the formation of the island group as such is quite

recent, not more than 5000 y ago, while some of the islands were formed during historical times, such as Telendos and Kalavros (see Triantis, 2006). The island group of Kalymnos is dominated by limestone, with scarce presence of schist (Triantafyllis & Karfakis, 1994).

#### SAMPLING

We visited the Astypalaia group during late April (2004) and late February (2005), and the Kalymnos group during late February (2004) and late March and early April (2005). Terrestrial isopods in the Aegean region exhibit a variety of biological cycles (Sfenthourakis, 1994). Thus, the 2 different sampling periods are important for a more or less complete knowledge of the islands' fauna. Collection was made by hand on 13 islands of the Astypalaia group and on 12 of the Kalymnos group. Additionally, we surveyed 13 sites on Astypalaia and 14 on Kalymnos, spread throughout the 2 islands, aiming at a complete coverage of the different habitat types (Figure 1 and 2). On the smaller islands, isopods were sampled from the whole area. Each locality was sampled by at least 2 experts until no new species were found. In addition to hand collecting, which is the most effective method

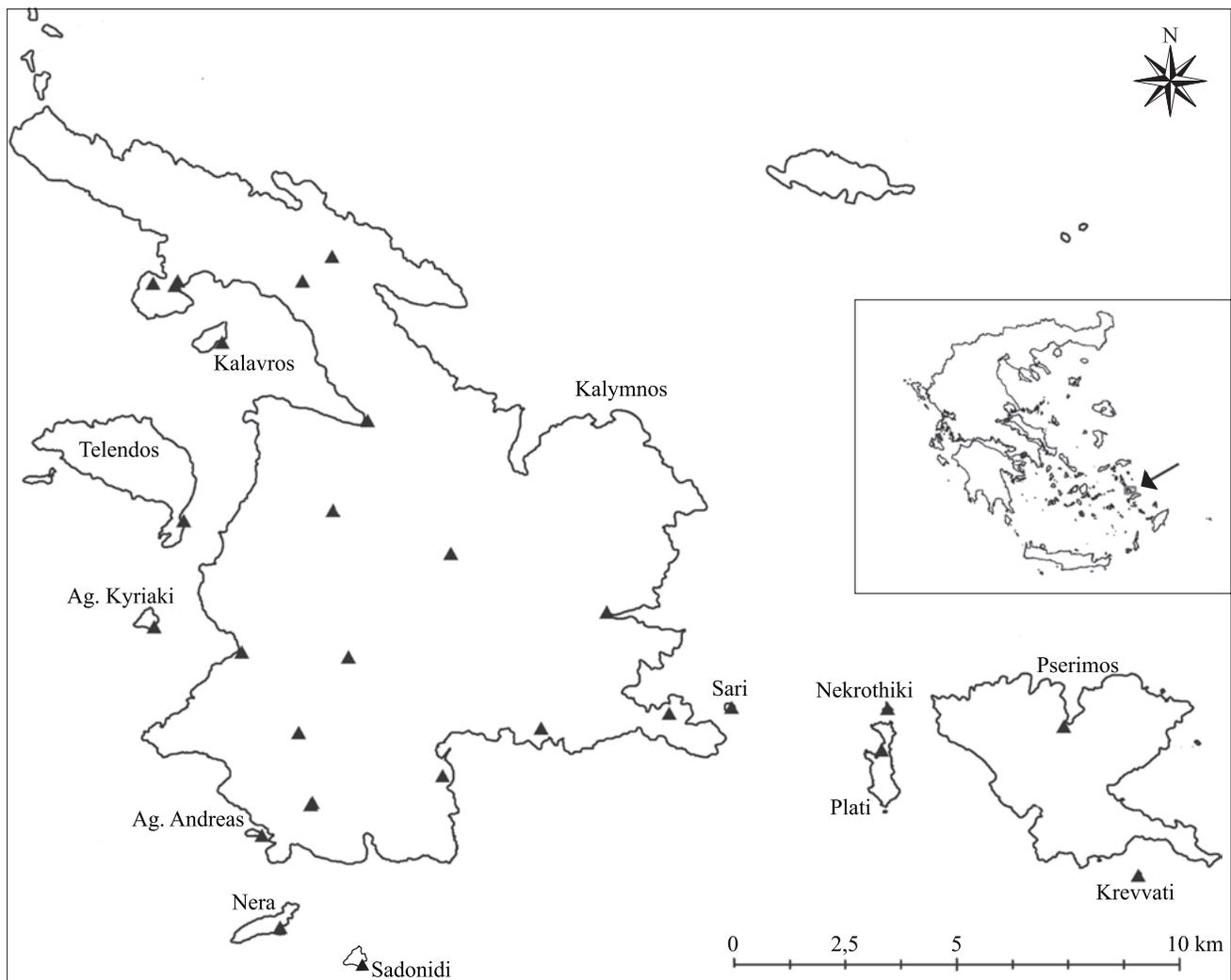


FIGURE 2. Map of the Kalymnos island group, its relative position in the Aegean, and the sampling stations.

for isopods in the Aegean area (Sfenthourakis, 1994), we put pitfall traps on the majority of islands, so as to cross-check the effectiveness of the collecting effort. Published data for the large islands were also taken into account (see Sfenthourakis, 1994; 1996a,b). All collections are deposited in the Natural History Museum of Crete.

ANALYSIS

The correlation of species richness (S) with a variety of variables was examined. These variables were area (A), altitude (Alt), distance from the main island (D), and environmental heterogeneity (H). Even though different measures of isolation can be applied (see Sfenthourakis, 1996a; Russell *et al.*, 2006), we preferred to use only the minimal distance of each islet from the main large island since both island groups are composed of a single large island with several small islands around it. Environmental heterogeneity was quantified by a proxy of habitat diversity measured as the number of identifiable habitat types preferred by terrestrial isopods. Habitat type identification was made according to the procedure of Sfenthourakis (1994; 1996a) and Sfenthourakis, Giokas, and Tzanatos (2004), with the exception of the 3 elevation classes used by these authors.

The standard methods of least-square regression and stepwise multiple regression were used to investigate the relationships between the dependent and the independent variables (see Tables I and II). All variables were log-transformed before analysis to ensure normality. As collinearity between independent variables may confound the analysis, we checked for redundancy by investigating tolerance levels for the variables for each separate analysis (for further discussion, see Hair *et al.*, 1998). The distance measure was log-transformed as  $\log(x + 0.01)$  since it is 0 for the 2 large islands.

Besides the well-established correlation among species richness and area, both theory and data suggest that both area and species richness are also often correlated with habitat diversity. In such cases, habitat diversity affects species richness directly, while the effects of area on species richness can be mediated either directly or indirectly, in the case of the latter through its correlation with habitat diver-

sity (see Kohn & Walsh, 1994; Ricklefs & Lovette, 1999; Triantis, Vardinoyannis & Mylonas, 2005; Triantis *et al.*, 2005). In order to discern these effects, we used semi-partial correlation to estimate (1) variance in species richness associated only with area (area's unique variance explanation); (2) variance in species richness associated only with habitat diversity (habitat diversity's unique variance explanation); and (3) variance in species richness explained by both area and habitat diversity (see Grace, 2006).

Despite the plethora of models proposed to describe the species-area relationship, herein we used only the most common, first suggested by Arrhenius (1921),

$$S = c \cdot A^z, \text{ or } \log S = c + z \log A \text{ in logarithmic scale} \quad [1]$$

mainly due to the fact that this particular model is the only one so far that contains parameters assigned with biological meaning (see Connor & McCoy, 1979). Since both island groups exhibit a considerable variance in size between large and small islands, we also applied the SPAR for the islets only (< 1 km<sup>2</sup>). We used a *t*-test (Zar, 1984) in order to compare the 2 resulting regression lines (all the islands and the "small islands", respectively). In addition to the SPAR, we also applied the Choros model (Triantis *et al.*, 2003; Triantis, Vardinoyannis & Mylonas, 2005; Triantis *et al.*, 2005). In the Choros model, an estimate of species richness is provided by the function,

$$S = c \cdot K^z, \text{ or } \log S = c + z \log K \text{ in logarithmic scale} \quad [2]$$

where K is the product of the multiplication of area with the number of habitat types present on the island. For comparison of the models, we used the *R*<sup>2</sup> values as a measure of goodness of fit. As the models have the same number of fitted parameters, *R*<sup>2</sup> values are comparable without any modification (Kvalseth, 1985). Nevertheless, we also report the values of the more general Akaike's Information Criterion (AIC), so as to strengthen the comparison between the 2 models (see Burnham & Anderson, 2002).

Even though the existence of the SIE is beyond doubt, its frequency of occurrence is still under debate (Lomolino & Weiser, 2001; Williamson, Gaston & Lonsdale, 2001; Gentile & Argano, 2005; Triantis *et al.*, 2006). The inclu-

TABLE I. Species richness (S), area (A), altitude (Alt), distance from the main island (D), and number of habitat types (H) for the islands of the Astypalaia island group.

Island	Area (km <sup>2</sup> )	Altitude (m)	Distance from the main island (km)	Species	Habitat types
Astypalaia	95.87	484.13	-	26	13
Ofidousa	1.912	122.71	10.25	12	6
Kounoupoi	1.445	86.53	3.68	11	8
Pontikousa	0.97	223.93	2.73	10	6
Fokionisi M.	0.57	48.14	1.77	8	4
Koutsomytis	0.47	55.16	2.4	11	8
Chondros	0.385	87.65	0.36	11	7
Ag. Kyriaki	0.255	21.09	2.02	8	4
Lianos	0.235	28.26	0.36	10	7
Fokionisi S.	0.090	44.21	0.49	6	3
Tigani	0.075	27.42	3.18	8	4
Fteno	0.019	< 10	3.89	8	4
Diapori	0.002	< 10	0.02	5	2

TABLE II. Species richness (S), area (A), altitude (Alt), distance from the main island (D), and number of habitat types (H) for the islands of the Kalymnos island group.

Island	Area (km <sup>2</sup> )	Altitude (m)	Distance from the main island (km)	Species	Habitat types
Kalymnos	110.8	668.52	-	22	11
Pserimos	14.63	265.41	4.74	15	10
Telendos	4.65	460.1	0.73	12	9
Plati	0.72	48.45	3.13	11	7
Nera	0.5	60.17	0.91	9	7
Kalavros	0.28	86.84	0.61	11	6
Ag. Kyriaki	0.15	54.92	1.04	6	4
Safonidi	0.15	< 10	4.45	6	4
Sari	0.03	< 10	0.40	7	3
Ag. Andreas	0.03	26.69	0.03	5	3
Nekrothiki	0.01	< 10	3.33	7	3
Krevvati	0.004	< 10	9.8	6	2

sion of a disproportionately high number of large islands in most biogeographical surveys could be one of the reasons why many studies have failed to detect the SIE (Lomolino & Weiser, 2001). In our study, the island size distribution for each archipelago shows a leptokurtic, right-skewed pattern, so no such bias is present. We applied the 3 methods so far proposed for the estimation of the upper limit of the SIE (see Lomolino & Weiser, 2001; Gentile & Argano, 2005; Triantis *et al.*, 2006). Lomolino and Weiser (2001) used a simple linear regression with a breakpoint transformation or a piecewise regression model to estimate the highest limit of the SIE. In this regression, the additive contribution of the independent variable to the prediction of the dependent one banks on a logical expression, so that, practically, different models are fitted to different portions of the data:

$$Y = b_0 + b_1 [(\log A - T) \times (\log A \geq T)] \quad [3]$$

where Y is species richness (that is, either S or logS for the semi-logarithmic or the logarithmic form of the species–area model, respectively), A is the island’s area (here measured in km<sup>2</sup>), T is the logA-threshold value that corresponds to the highest area limit for the small island effect, and  $\log(A) \geq T$  is a logical expression that returns the value of 0 or 1. For all islands that are smaller than T, the independent variable is 0 and species richness is estimated as an intercept ( $b_0$ ), independently of area. On larger islands, where logA is higher than T, the independent variable is equal to the difference between logA and the breakpoint T.

Gentile and Argano (2005) used a discontinuous model, which combines 2 linear relationships into a single equation:

$$Y = (b_0 + b_1 \log A) \times (\log A \leq T) + (b_2 + b_3 \log A) \times (\log A > T) \quad [4]$$

The dependent variable Y, and the independent ones, A and T, are defined as in equation [3]. There is one logical expression for each of the 2 combined linear relationships,  $\log(A) \leq T$  and  $\log A > T$ , that return the value of 0 for false and 1 for true. This model does not assume *a priori* the existence of an SIE. If a breakpoint is found, the correlation between logS and logA to the left of the breakpoint can still be evaluated, whereas this is not possible if equation 3 is used. The parameters were estimated by using nonlinear estimation procedures based on iteration. The breakpoint values were incremented by 0.1. Values of all parameters were chosen on the basis of the amount of variance explained (maximum  $R^2$  value).

Triantis *et al.* (2006) used a method based on path analysis using an *a priori* model according to which area (A) directly affects habitat diversity (H) and both these variables directly affect species number per island (S). The data set is studied to detect whether there is a certain island size under which the direct effects of area are eliminated. The detection is carried out through the sequential exclusion of islands from the largest to the smallest and the simultaneous estimation of standardized partial regression coefficients of area ( $b_A$ ). When  $b_A$  is found to be  $b_A < 0$ , the respective area is assigned as the upper limit of SIE, symbolized by L. According to Triantis *et al.* (2006) the SIE is present when the direct and/or the total effects of area on species richness are eliminated (for further details see Triantis *et al.*, 2006).

For the exploration of nestedness patterns we used the Nestedness Temperature Calculator (Atmar & Patterson, 1993; 1995). Higher temperatures are indicative of lower community nestedness, while “colder” matrices are more nested. The free software developed by these authors calculates a “Temperature” value (T) for each community and offers the possibility of a Monte Carlo simulation for assessing the statistical significance of this value. The software also provides the “idiosyncratic temperatures” of each island and species. These values correspond to the contribution each island and each species makes to the destruction of perfect nestedness. The “Temperature” method has been widely used in the literature and has become a familiar tool to many researchers, though its limitations should always be kept in mind (Fischer & Lindenmayer, 2002). Recently, this method has received a lot of criticism regarding the validity of the nestedness assessment it provides, mainly on the basis of the assumptions it uses for the construction of “null” matrices for the statistical evaluation of the temperature values (Rodríguez-Gironéz & Santamaría, 2006; Greve & Chown, 2006). Even though we agree with these criticisms, we still preferred to use this method since we were not interested in an absolute measurement of nestedness levels but only in comparing the behaviour of 2 similar data sets. Also, we were interested in exploring the “idiosyncratic temperatures” output provided by this software. In any case, and since Temperature is affected also by matrix size (Wright *et al.*, 1998; Rodríguez-Gironés & Santamaría, 2006), for comparative purposes we also applied the standardized metric C of Wright and Reeves (1992), which has better behaviour in relation to matrix size. This metric of nestedness is calculated as

$$C = (N_c - E[N_c]) / (\max[N_c] - E[N_c]) \quad [5]$$

where  $N_c$  is the sum over species and sites of the number of times a species’ presence at a site correctly predicts its presence at richer sites,  $E[N_c]$  is the expected value of  $N_c$ , and  $\max[N_c]$  is the maximum value that  $N_c$  would take if the matrix were perfectly nested. These values are calculated through the row and column totals of each matrix (for a simple presentation see Hunter, 2004). Values of C near 1 denote high nestedness, while values near 0 are obtained when nestedness does not deviate from random expectations. Negative values might be obtained when a matrix is less nested than expected by chance. The statistical significance of C is given by Cochran’s Q test for equality of species incidences, as suggested by Wright and Reeves (1992) and applied by several authors ever since (Yiming, Niemelä & Dianmo, 1998; Hunter, 2004).

All the metrics were applied for both the sum of all islands and the small islands alone, following the analysis applied to the SPAR (see above). The statistical program STATISTICA (version 5.1, StatSoft, Inc., Tulsa, Oklahoma, USA) was used.

## Results

The species present on each island and the total number of species, area, elevation, and number of habitats of each island are presented in Appendices I and II and in Tables I and II. The relationship between species richness

and area according to SPAR was high for both island groups (Table III). The results of the simple correlations between species richness, area, habitat diversity, altitude, and geographical isolation are shown in Tables IV and V for the Astypalaia and Kalymnos groups, respectively.

Tolerance values were adequately high (that is, more than 0.10) for all but 3 pairs of variables across the 2 island groups. Collinearity was detected within the analyses of both island groups. For the island group of Astypalaia, we detected a strong positive correlation between island area and island altitude ( $r = 0.926$ ,  $P < 0.001$ ), and therefore we excluded island altitude from the multiple regression. Nevertheless, we have to note that the relationship between

TABLE III. The results of the comparison between the classic species-area model (SPAR) and the Choros model.  $z$  and  $c$  are the respective parameters for the 2 models. \*:  $P < 0.01$ , n.s.:  $P \geq 0.05$ .  $\Delta AIC$  is the difference between the AIC values of the 2 models [ $\Delta AIC = AIC(\log S - \log A) - AIC(\log S - \log K)$ ]. A positive value of  $\Delta AIC$  indicates that the Choros model is superior to the classic SPAR.

Island group	Model	$z$	$c$	$R^2$	$\Delta AIC$
Astypalaia	SPAR	0.144	11.2	0.84*	3.541
	Choros	0.126	8.9	0.88*	
Astypalaia (small islands)	SPAR	0.110	10.3	0.62*	3.419
	Choros	0.100	8.7	0.73*	
Kalymnos	SPAR	0.133	10.4	0.81*	0.445
	Choros	0.113	8.4	0.82*	
Kalymnos (small islands)	SPAR	0.110	9.49	0.42*	0.692
	Choros	0.087	8.08	0.46*	

TABLE IV. The results of the simple regressions ( $r$ ) of species richness (S) with area (A), altitude (Alt), distance (D), and habitat diversity (H) and of the independent variables for the island groups of Astypalaia and Kalymnos. \*:  $P < 0.01$ , ns;  $P \geq 0.05$

		A	Alt	D	H
Astypalaia group	S	0.915*	0.971*	0.209 ns	0.937*
	A		0.926*	0.009 ns	0.864*
	Alt			0.002 ns	0.783*
	D				0.054 ns
Kalymnos group	S	0.900*	0.807*	0.307 ns	0.917*
	A		0.926*	0.395 ns	0.973
	Alt			0.02 ns	0.935
	D				0.321 ns

TABLE V. Results of the study of the small island effect (SIE). For each of the 3 methods applied, upper limit,  $R^2$ , improvement of fit compared to the classic species-area models, and number of islands included in the SIE are presented. For the method of Triantis *et al.* (2006),  $R^2$  and improvement of fit are not presented since the method is not comparable to the classic species-area relationships (see text).

Method	Island group	Upper limit of SIE (km <sup>2</sup> )	$R^2$	Improvement of fit	No. of islands included in SIE
Lomolino & Weiser, 2001; $\log S - \log A$	Astypalaia	0.04	0.838	-	2
	Kalymnos	0.06	0.837	0.027	4
Lomolino & Weiser, 2001; $S - \log A$	Astypalaia	0.168	0.897	0.151	4
	Kalymnos	0.113	0.921	0.106	4
Gentile & Argano, 2005; $\log S - \log A$	Astypalaia	0.347	0.863	0.025	6
	Kalymnos	1	0.830	0.020	9
Gentile & Argano, 2005; $S - \log A$	Astypalaia	0.03	0.889	0.143	2
	Kalymnos	1	0.915	0.099	9
Triantis <i>et al.</i> , 2006	Astypalaia	0.47	-	-	8
	Kalymnos	14.63	-	-	11

area and number of habitats was also significantly high (Table IV). For the island group of Kalymnos, we detected a strong positive correlation between island area, island altitude, and number of habitats (Table IV); we excluded island altitude and area from the multiple regression since number of habitats exhibited higher correlation with species richness. According to the stepwise regressions for Astypalaia, both area and habitat diversity entered the final model with the effects of distance being statistically insignificant. The percentage of total variance explained by the best model was very high (95%). According to the stepwise regressions for Kalymnos, only habitat diversity entered the final model, with the effects of distance being statistically insignificant. The percentage of total variance explained by the best model was also very high (84%).

To further check that our results were not simply artifacts of our forward stepwise regression procedure, we also performed standard multiple regressions including all the independent variables regardless of multicollinearity. This procedure produced results similar to those of the forward stepwise regressions. Hence, the results from the stepwise multiple regression analyses were not simply caused by random inflation of independent variables (see Hair *et al.*, 1998).

Based on the semipartial correlation analysis used to separate the effects of area and environmental heterogeneity on species richness, we calculated that for both island groups species richness was mainly associated with the effects of both area and habitat diversity while the net effects of area and habitat diversity alone were quite low. For the Astypalaia group, 4% of species richness was associated only with area, 8.5% was associated with environmental heterogeneity, 78% was explained by both area and environmental heterogeneity, and 9.5% percent of the variance remained unexplained. For the Kalymnos group, 1% was associated only with area, 3% with environmental heterogeneity, 81% was explained by both area and environmental heterogeneity, and 12% percent of the variance remained unexplained.

The Choros model, which includes both area and habitat diversity, performed better than the classic SPAR in terms of its predictive power on species richness, but the increase of fit was relatively small (Table III).

The results of the analyses for detection of an SIE and estimation of its upper limit based on the 3 different methods are shown in Table V. It is clear that the methods of Lomolino and Weiser (2001) and Gentile and Argano (2005) gave quite different results. The logS-logA form of the 2 methods resulted in a low increase of fit compared to the classic equation of the SPAR (2–3%), while the S-logA form offered a quite significant increase (10–15%). Regardless of the fit of each method, an SIE was detected for both island

TABLE VI. Results of nestedness analysis according to the “Temperature” value and the C metric for both island groups with and without the large “source” island. T = temperature of each matrix, P = probability level, F = matrix fill, N = matrix size (species × islands).

	T	P	F	N	C	Cochran Q
ASTYPALAI A						
All	12.03	< 0.03	25.1	32 × 13	0.80	186*
Islets only	24.98	0.055	31.5	22 × 12	0.68	135.93*
KALYMNOS						
All	11.54	< 0.05	32.2	26 × 12	0.75	154.08*
Islets only	23.8	ns	42.7	15 × 9	-0.58	61.17*

\* P < 0.001; ns

groups. Following the method of Triantis *et al.* (2006) the phenomenon was detected in both island groups, but with a different number of islands included (Table V).

According to both the “Temperature” metric and the C metric, both island groups are highly nested (see Table VI) and exhibit similar values of nestedness. As expected, nestedness becomes marginally significant or destroyed when the largest islands (> 1 km<sup>2</sup>) of each group are excluded. In fact, the C metric becomes negative for the Kalymnos group (while T is non-significant), indicating less nestedness than expected by chance. The rank order of “idiosyncratic temperatures” (a measure of their effect on the destruction of perfect nestedness) of islands is not related to their species richness (non-significant Spearman rank correlation coefficients) for any island group (Table VII), while the rank orders of the complete data set and the one without the large island are significantly correlated for each island group (Table VIII), meaning that the same islets more or less contribute to the deviation from a perfectly nested pattern.

The species that exhibit large “idiosyncratic temperature” values are similar among the complete and islets-only data sets, within each island group (Table IX). The “top-10” species according to their idiosyncratic temperature in the

TABLE VII. The rank order of islands according to their “idiosyncratic temperatures” and their respective species richness, for both island groups with and without their large “source” island. The Spearman rank correlation coefficients among ranks and species richness were non-significant for all pairs.

Astypalaia				Kalymnos			
All		Islets only		All		Islets only	
Idiosyncratic rank	Species richness						
1	6	1	12	1	5	1	5
2	5	2	6	2	6	2	6
3	12	3	11	3	6	3	9
4	8	4	5	4	22	4	15
5.5	26	5	8	5	9	5	12
5.5	11	6.5	10	6	7	6	6
7	8	6.5	8	7	12	7	11
8	8	8	11	8	15	8	7
9	10	9	8	9.5	11	9	7
10	10	10	11	9.5	7	10	11
11	11	11	10	11	11	11	6
12.5	11	12	8	12	6		
12.5	8						

TABLE VIII. The islands of each group ranked according to their idiosyncratic temperatures, and the correlation among these ranks within each group.

Astypalaia		Kalymnos	
All	Islets only	All	Islets only
Diapori	Ofidousa	Ag. Andreas	Ag. Andreas
S. Fokionisi	Diapori	Krevvati	Krevvati
Ofidousa	Chondros	Ag. Kyriaki	Nera
Ag. Kyriaki	S. Fokionisi	Kalymnos	Pserimos
Chondros	M. Fokionisi	Nera	Telendos
Astypalaia	Lianos	Nekrothiki	Ag. Kyriaki
M. Fokionisi	Fteno	Telendos	Kalavros
Fteno	Koutsomytis	Pserimos	Nekrothiki
Pontikousa	Tigani	Sari	Sari
Lianos	Kounoupoi	Kalavros	Plati
Kounoupoi	Pontikousa	Plati	Safonidi
Koutsomytis	Ag. Kyriaki	Safonidi	
Tigani			
Spearman rank correlation coefficient: 0.62 (P < 0.05)		Spearman rank correlation coefficient: 0.83 (P < 0.02)	

TABLE IX. Species ranked according to their “idiosyncratic temperatures” (first 10 positions) for each island group.

Astypalaia		Kalymnos	
All	Islets only	All	Islets only
<i>Armadillo officinalis</i>	<i>Schizidium hybridum</i>	<i>Armadillidium granulatum</i>	<i>Armadillidium granulatum</i>
<i>Armadillo tuberculatus</i>	<i>Armadillo tuberculatus</i>	<i>Platyarthus schoeblii</i>	<i>Platyarthus schoeblii</i>
<i>Schizidium oertzeni</i>	<i>Armadillo officinalis</i>	<i>Porcellio obsoletus</i>	<i>Porcellio flavomarginatus</i>
<i>Proporcellio quadriseriatus</i>	<i>Schizidium oertzeni</i>	<i>Leptotrichus kosswigi</i>	<i>Porcellio obsoletus</i>
<i>Platyarthus schoeblii</i>	<i>Rodoniscus anophthalmus</i>	<i>Porcellio lamellatus</i>	<i>Porcellio lamellatus</i>
<i>Porcellio lamellatus</i>	<i>Platyarthus schoeblii</i>	<i>Porcellio flavomarginatus</i>	<i>Leptotrichus kosswigi</i>
<i>Leptotrichus kosswigi</i>	<i>Leptotrichus kosswigi</i>	<i>Paraschizidium</i> sp.1	<i>Platyarthus lindbergi</i>
<i>Armadillidium ameglioi</i>	<i>Tylos ponticus</i>	<i>Agabiformius lentus</i>	<i>Paraschizidium</i> sp.1
<i>Echinarmadillidium cycladicum</i>	<i>Proporcellio quadriseriatus</i>	<i>Protracheoniscus kalymnius</i>	<i>Protracheoniscus kalymnius</i>
<i>Leptotrichus naupliensis</i>	<i>Armadillidium ameglioi</i>	<i>Platyarthus lindbergi</i>	<i>Tylos ponticus</i>

different data sets give a measure of community homogeneity. For the Kalymnos group, this list contains 9 species in common, while for the Astypalaia group only 7 species in common are included. What is more interesting, the species with high “idiosyncratic temperatures” are very different between the 2 island groups. Only 2 species, *Leptotrichus kosswigi* and *Platyarthus schoeblii*, are consistently present in the top-10 positions of “idiosyncratic temperatures”, regardless of the fact that the 2 island groups have 17 species in common.

### Discussion

The slopes of the SPARs for terrestrial isopods of the 2 groups are almost identical, 0.144 and 0.133 for the Astypalaia and Kalymnos groups, respectively, and place the 2 island groups within the intra-provincial category *sensu* Rosenzweig (1995). Similar z-values are found when we compare the diversities of differently-sized parts of a province. They result from the accumulation of habitat heterogeneity within a province as we sample larger and larger fractions of it. The low z-values of the 2 island groups are the anticipated result of their “recent” formation. Despite their different geological histories, both were formed recently in geological time (Dermitzakis, 1990; Lambeck, 1996; Perissoratis & Conispoliatis, 2003). This “recent” formation has resulted in small islands that still behave as parts of a continuous land mass; consequently, the reduction of area has not yet led to a significant loss of species (Terborgh & Winter, 1980; Karr, 1982). The presence of species such as *Armadillo officinalis* and *Porcellio obsoletus* on these small islets is unusual; they are absent from the vast majority of Aegean islets (Sfenthourakis, 1994). A characteristic example is the presence of *A. officinalis* on the smallest islet of the Astypalaia group (Diapori), and another is the presence of *P. obsoletus* on the smallest islet of the Kalymnos group (Krevvati) (see Appendices I and II).

The short distances between islets and the long human presence contribute to this continental behaviour, as the probability of new immigrants reaching the islands is high despite the low dispersal ability of terrestrial isopods. Hence, z-values remain within the intra-provincial rather than the inter-island range. Furthermore, despite the fact that terrestrial isopods in general exhibit low dispersal abilities, the species present on the 2 island groups have broad distributions, something that can be considered an indication that these particular species are effective dispersers

(Triantis, 2006). This may be an additional reason for the reduction of the “island character” of these groups as far as terrestrial isopods are concerned, which is another explanation of the low z-values.

All the above are validated by the fact that the z-values arising from the SPARs after the exclusion of the largest islands are similar to those of the complete data sets (Table III). Also, the strength of the correlation between species number and area is very high in both cases (see Table IV). Hence, the 2 island groups exhibit uniform behaviour as far as the relation of terrestrial isopods species and their total area is concerned.

The Choros model has more explanatory power than area alone. While the increase in fit ( $R^2$ ) is not great (Table III), our results are in accordance with the findings of Triantis *et al.* (2003; 2005) and Triantis, Vardinoyannis, and Mylonas (2005), showing that the increased fit of Choros over area alone is relatively consistent. A significant increase in the fit of the Choros model is expected when area and the measure of environmental heterogeneity are significantly decoupled (see Triantis, Vardinoyannis & Mylonas, 2005; Triantis *et al.*, 2005). Such a case is represented by the small islands of the Astypalaia group, where the relationship between island area and number of habitat types is relatively low ( $R^2 = 0.651$ ,  $P < 0.01$ , when in all other cases it remained higher than 0.86). The utility and novelty of the Choros model are not necessarily due to the better fit to observed data but arise from the relative simplicity of the technique, as well as the increased explanatory power of the model. The main shortcoming of the model lies in the standardization of habitat diversity approach, and thus choros ( $K$ ), across studies. Nevertheless, the effectiveness of the model so far is a clear indication that the inclusion of measures of environmental heterogeneity is crucial for models attempting to explain variation in species richness. However, caution is necessary in the use of proxy measures of habitat diversity since, if they are not informed by the natural history of the taxon under study, they can reduce the effectiveness of the model and may lead to an underestimation of the effects of environmental heterogeneity (Triantis, Vardinoyannis & Mylonas, 2005; Triantis *et al.*, 2006; Panitsa *et al.*, 2006).

Area and number of habitats are strongly interconnected (see Rosenzweig, 1995; Triantis *et al.*, 2003). The strong intercorrelation of area and habitat diversity likely results from the interdependence of area and the presence of specific

habitat types (Kohn & Walsh, 1994). Certain habitat types only occur on the largest islands of the 2 island groups, such as small streams, and other habitats, such as those associated with beaches and anthropogenic biotopes (e.g., cultivation, settlements), are not found on the smaller islands (Sfenthourakis, 1996b; Triantis, 2006). Consequently, species strongly dependent on these habitat types are absent from the smaller islands (e.g., *Graeconiscus thermophilus*, *Trichoniscus rhodiensis*, *Nagurus aegaeus*). The results of the semipartial correlation analysis indicate that the species richness variance is primarily explained by the intercorrelation of area and habitat diversity, while the net effects of area and environmental heterogeneity are quite low. These results are in accordance with the results of Triantis *et al.* (2005) studying the land snails of another island group in the Aegean. The low net effects of area are strongly connected to the reduced possibility of extinction of species in the studied island groups. According to Ricklefs and Lovette (1999), area influences species richness directly in 2 different ways: larger islands offer larger targets for dispersing individuals, and in general, larger islands support larger populations, which have reduced chances of extinction. In the first case, apart from the largest island in each group, all the islands have similar areas and are close to the main island, and thus area is not expected to play an important role in the immigration rate. Furthermore, area is not expected to affect the size of isopod populations except on very small islets (Sfenthourakis, 1994), so the direct effects of area remain marginal.

According to the highest  $R^2$  value, an SIE is present in the Astypalaia group including 4 islets (semi-log model of Lomolino & Weiser, 2001), and the same also applies to the Kalymnos group (semi-log model of Lomolino & Weiser, 2001) (Table V). In all cases, the method of Gentile and Argano (2005) detected an SIE, but the improvement of fit was lower than that of Lomolino and Weiser (2001). According to Gentile and Argano (2005), the equation proposed by Lomolino and Weiser (2001) (equation [3]) is biased, because it assumes *a priori* an SIE and imposes it on the model. Therefore, although it depicts the species–area relationship more thoroughly, it is not appropriate for the detection of an SIE. Note that according to Lomolino and Weiser (2001), the SIE was detected in 90 out of 101 data sets studied (semi-log model), and 7 of the 11 cases where the phenomenon was absent included only large islands (*i.e.*, exceeding 2 km<sup>2</sup>). Hence, with this method, an SIE is almost always detected. In this respect the model of Gentile and Argano (2005) is superior, since it does not assume *a priori* the existence of an SIE. If a breakpoint is found, the correlation between species number and area to the left of the breakpoint can still be evaluated. This is in accordance with Williamson, Gaston, and Lonsdale (2001) and Triantis *et al.* (2006), who noted that the left hand of the species–area relationship exhibits variable behaviour, ranging from being flat, to following the linearity of larger islands, to being steep.

Yet, the methods of Lomolino and Weiser (2001) and Gentile and Argano (2005) have some important shortcomings. The first is related to the fact that only area is used for the detection of the SIE, when it has been long established that factors such as environmental characteristics, interspe-

cific interactions, stochastic events, habitat diversity, isolation, occasional disturbances, and human impact might be more important to the establishment of species richness on small islands (Whittaker, 1998; Lomolino & Weiser, 2001). The second is related to the fact that the threshold value estimated might be influenced by large gaps occurring in the area range of islands sampled (see Gentile & Argano, 2005). The basic advantages of the method proposed by Triantis *et al.* (2006) are inclusion of environmental heterogeneity and independence of the method from the classical species–area relationships. This leads to the recognition of two distinct SIE patterns: (1) the classical SIE, where both the direct and the indirect effects of area are eliminated, and (2) the cryptic SIE, where area affects species richness indirectly (see Triantis, 2006; Triantis *et al.*, 2006). According to the method of Triantis *et al.* (2006), a cryptic SIE is present on both island groups, with the upper limit for Kalymnos group (14.67 km<sup>2</sup>) being higher than the corresponding limit of Astypalaia (0.47 km<sup>2</sup>, Table V). It is important to note here that the methods of Triantis *et al.* (2006) and Gentile and Argano (2005) resulted in a similar trend with respect to the number of islands included in the SIE. The phenomenon is restricted to the smaller islands in the Astypalaia group, while almost all islands of the Kalymnos group are included. The method of Lomolino and Weiser (2001), by contrast, resulted in identical numbers of islands for both island groups without any discrimination (see Table V).

Based on the results of Triantis *et al.* (2006), the difference between the 2 upper limits is related to the 3 distinctive characteristics of the island groups: a) Kalymnos' islands were formed more recently than the Astypalaia island group; b) the Astypalaia group is in one of the most isolated areas of the Aegean Sea, while Kalymnos lies near Leros island and the Turkish coasts; and thus c) the Kalymnos group is affected by a significantly larger “species pool” than the Astypalaia group. The longer existence of the Astypalaia island group and its greater isolation contribute to the “increase” in the “island character” of this group for terrestrial isopods, while the Kalymnos group, affected by the nearby islands and the Turkish coast, still exhibits an intense “mainland character”, where area affects species richness only indirectly (see Rosenzweig, 1995). Although the net contribution of area to species richness is quite low in both island groups, for the Kalymnos group it is only 1%. Thus, when the largest island is removed from that group, the net contribution of area is eliminated and an SIE is detected. In the case of the Astypalaia group, on the other hand, area continues to have a small effect for the largest islands; this effect is eliminated only when we reach the smaller islands, and thus we observe an SIE for islands smaller than 0.47 km<sup>2</sup>. Nevertheless, the difference between the 2 island groups with respect to the upper limit of the SIE cannot be considered significant. The similarity of the 2 island groups is also validated by the temperatures of nestedness of the two. Both methods used calculated very low values, which are almost equal for the 2 groups, indicating highly nested faunas. The same outcome occurs when only the small islands of the groups are considered: although an anticipated increase of temperature values is observed, these values remain almost the same (Table VI). The nestedness analysis is also quite informative with respect to structure similarities

between the isopod faunas of the 2 groups. The rank order of “idiosyncratic temperatures” of islands is not related to their species richness for any island group (Table VIII), indicating that all the islands in both groups exhibit more or less the same behaviour. Moreover, the rank orders of both the complete data set and the set with the small islands only are significantly correlated for each island group (Table IX), meaning that the same islets more or less contribute to the deviation from a perfectly nested pattern. Thus, despite the fact that the species with high “idiosyncratic temperatures” are very different between the 2 island groups, similar overall patterns arise. The Kalymnos group becomes more “unordered” after the exclusion of larger islands, indicating a more variable isopod fauna, apparently due to its more recent formation (less time available for relaxation) and, of course, the significant effect of the nearby “species pools”.

Concluding, we have to note that the 2 island groups studied are characteristic examples of the various island groups spread in the Aegean Sea. The majority of the island groups in the Aegean were formed quite recently in geological time, and even for taxa with reduced dispersal ability, the islands still “behave” as parts of a continuous land mass, with large numbers of species even on the smallest islands, marginal extinctions, limited net effects of island size, and a significant contribution of the interrelationship between area and environmental heterogeneity (see also Triantis *et al.*, 2005). Hence, the geological history of the area’s isolation is not crucial to the number of species present; its role is mainly restricted to the percentage of endemism and the faunal composition of insular communities. Our data reveal that recent processes are shaping biodiversity in the well-defined small island groups dominating the Aegean, causing island groups with different geological histories to exhibit similar patterns. Further testing of this pattern may provide insights crucial for the increasing number of conservation efforts in the area of the Aegean Sea and the eastern Mediterranean Sea.

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APPENDIX I. The distribution of terrestrial isopods on the islands of the Astypalaia island group. In 3 cases, we were not able to identify the specimens to the species level due to the absence of male representatives, which have the species-specific characteristics. These cases are *Trichoniscus* sp. (either *T. oedipus* or *T. pygmaeus*) for the islands Kounoupoi and Koutsomytis (Astypalaia group), *Leptotrichus* sp. (either *L. kosswigi* or *L. nauplensis*) for Ag. Kyriaki (Astypalaia group), and *Chaetophiloscia* sp. (*C. lagoi* or *C. cellaria*) for the islands Pserimos, Telendos, Plati, and Nera (Kalymnos group).

Species	Astypalaia	Ofidousa	Kounoupoi	Pontikoussa	Fokionisi M.	Koutsomytis	Chondros	Ag. Kyriaki	Lianos	Fokionisi S.	Tigani	Eteno	Diapori
<i>Tylos ponticus</i> Grebnicki, 1874	1								1				
<i>Ligia italica</i> Fabricius, 1798	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Trichoniscus oedipus</i> Sfenthourakis, 1995	1		1			1							
<i>Trichoniscus pygmaeus</i> Sars, 1898	1												
<i>Stenoniscus pleonalis</i> Aubert and Dollfus, 1890	1												
<i>Armadilloniscus aegaeus</i> Schmalzfuss, 1981	1												
<i>Halophiloscia couchi</i> Kinahan, 1858	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Halophiloscia hirsuta</i> Verhoeff, 1928							1						
<i>Stenophiloscia vandeli</i> Matsakis, 1967	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Rodoniscus anophthalmus</i> Arcangeli, 1934	1	1			1		1		1		1		
<i>Bathytropa granulata</i> Aubert and Dollfus, 1890	1												
<i>Chaetophiloscia lagoi</i> Arcangeli, 1934	1		1			1							
<i>Platyarthrus lindbergi</i> Vandel, 1959	1												
<i>Platyarthrus schoeblii</i> Budde-Lund, 1885	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Agabiformius lentus</i> Budde-Lund, 1885	1	1							1				
<i>Leptotrichus kosswigi</i> Strouhal, 1960	1							1				1	
<i>Leptotrichus naupliensis</i> Verhoeff, 1901	1		1	1	1	1			1				
<i>Porcellio laevis</i> Latreille, 1804	1												
<i>Porcellio lamellatus</i> Budde-Lund, 1885	1			1			1	1					
<i>Porcellio obsoletus</i> Budde-Lund, 1885	1												
<i>Porcellionides pruinosus</i> Brandt, 1833	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Proporcellio vulcanius</i> Verhoeff, 1908		1											
<i>Nagurus aegaeus</i> Schmalzfuss, 1977	1												
<i>Armadillidium marmoratum</i> Strouhal, 1929	1												
<i>Armadillidium vulgare</i> Latreille, 1804	1												
<i>Armadillidium ameglioii</i> Arcangeli, 1914		1		1									
<i>Echinarmadillidium cycladicum</i> Schmalzfuss and Sfenthourakis, 1995		1		1									
<i>Paraschizidium</i> sp1.			1			1	1						
<i>Schizidium oertzeni</i> Budde-Lund, 1896			1		1	1					1	1	
<i>Schizidium hybridum</i> Budde-Lund, 1896	1	1											
<i>Armadillo officinalis</i> Duméril, 1816	1												1
<i>Armadillo tuberculatus</i> Vogl, 1876	1	1	1	1	1	1	1	1	1	1	1	1	
Total	26	12	11	10	8	11	11	8	10	6	8	8	5

APPENDIX II. The distribution of terrestrial isopods on the islands of the Kalymnos island group.

Species	Kalymnos	Pserimos	Telendos	Plati	Nera	Kalavros	Ag. Kyriaki	Safonidi	Sari	Ag. Andreas	Nekrothiki	Krevvati
<i>Tylos ponticus</i> Grebnicki, 1874	1	1	1	1	1						1	
<i>Ligia italica</i> Fabricius, 1798	1	1	1	1	1	1	1	1	1	1	1	1
<i>Graeconiscus thermophilus</i> Çağlar, 1948	1											
<i>Trichoniscus rhodiensis</i> Arcangeli, 1934	1											
<i>Stenoniscus pleonalis</i> Aubert and Dollfus, 1890	1											
<i>Halophiloscia couchi</i> Kinaha1, 1858	1	1	1	1	1	1	1	1	1	1	1	1
<i>Stenophiloscia vandeli</i> Matsakis, 1967	1	1	1	1	1	1	1	1	1	1	1	1
<i>Chaetophiloscia cellaria</i> Dollfus, 1884	1	1	1	1		1						
<i>Chaetophiloscia lagoi</i> Arcangeli, 1934	1											
<i>Chaetophiloscia elongata</i> Dollfus, 1884	1											
<i>Platyarthrus lindbergi</i> Vandel, 1959	1					1						
<i>Platyarthrus schoeblii</i> Budde-Lund, 1885	1	1				1	1					1
<i>Agabiformius lentus</i> Budde-Lund, 1885		1										
<i>Leptotrichus kosswigi</i> Strouhal, 1960	1	1	1	1	1	1		1	1	1	1	1
<i>Porcellio laevis</i> Latreille, 1804	1											
<i>Porcellio lamellatus</i> Budde-Lund, 1885				1							1	
<i>Porcellio obsoletus</i> Budde-Lund, 1885	1	1	1									1
<i>Porcellio flavomarginatus</i> Lucas, 1853					1							
<i>Porcellionides pruinosus</i> Brandt, 1833	1	1	1	1	1	1	1	1	1			
<i>Proporcellio vulcanius</i> Verhoeff, 1908	1											
<i>Protracheoniscus kalymnius</i> Sfenthourakis, 1995	1	1		1		1			1			
<i>Armadillidium granulatum</i> Brandt, 1833	1	1	1	1	1	1	1	1		1	1	
<i>Armadillidium marmoratum</i> Strouhal, 1929	1	1	1									
<i>Paraschizidium</i> sp2.			1									
<i>Schizidium hybridum</i> Budde-Lund, 1896	1	1	1	1	1	1			1			
<i>Armadillo officinalis</i> Duméril, 1816	1	1										
Total	22	15	12	11	9	11	6	6	7	5	7	6