



Habitat diversity, ecological requirements of species and the Small Island Effect

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ABSTRACT

Aim To explore the causal factors leading to a significant Small Island Effect (SIE), that is, the absence of the commonly found species–area relationships below an island size, on the terrestrial isopod communities from a large number of islands.

Location Ninety islands of the Aegean Sea (Greece).

Methods The detection of a significant SIE is assessed through the application of all three methods available in the literature. Species are divided into generalists and specialists. We tested if the minimum area and the area range of each species' occurrences differ between generalists and specialists. Next, we searched for differences in the ratios of specialists to generalists above and below the SIE threshold, and tested their cumulative ratios when islands are arranged according to increasing area, altitude or habitat diversity in order to identify the threshold where they become statistically indistinguishable from the ratio of the total set of islands.

Results Our results indicate a strong effect of habitat availability on the SIE. Communities of islands within the SIE range, host a higher percentage of generalists. An analysis of the specific habitat requirements shows that, for isopods, the crucial factor is the lack of habitats related to inland waters from small islands.

Main conclusions The distribution of habitats on islands of different size is of major importance for the occurrence of a SIE. The relative representation of specialist and generalist species on islands of different size plays an important role in shaping SIE-related patterns. Conservation efforts should pay special attention on freshwater habitats, especially on small Aegean islands. Identifying the causal factors of SIE, combined with a thorough knowledge of the ecological requirements of species can offer insights into identifying habitat types and groups of species that are more vulnerable to alterations of the environment.

Keywords

Aegean, area range of occurrence, generalists, island biogeography, isopods, minimum area of occurrence, specialists.

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INTRODUCTION

Within the island biogeography paradigm there has been an ongoing discussion on the special patterns exhibited by very small islands that often lead to an apparent Small Island Effect (hereafter SIE), that is, the absence of the commonly found relationship of island area and species richness below an island size that depends on the taxon and the archipelago studied. A discussion of an idiosyncratic 'behaviour' of small islands and islets had been originally made by Preston (1962) and Wiens (1962), while a more explicit exposition of the pattern was made by Niering (1963). MacArthur & Wilson (1967) also discussed the subject, but the SIE was addressed as such by Whitehead &

Jones (1969). Several authors dealt with the SIE afterwards (see Triantis *et al.*, 2006 for a review) but explicit models for its detection were presented only by Lomolino & Weiser (2001), Gentile & Argano (2005) and Triantis *et al.* (2006). Clarification of the causal factors underlying the SIE is of great interest to conservation biology since small islands are vulnerable unique ecosystems where even small perturbations may have large effects to species richness and composition.

Two related explanations, probably complementary, have been offered to explain the SIE: habitat diversity/quality and differences in extinction rates. The first argues that there is a 'threshold' area below which the presence or the absence of certain habitat types is the major driver of species richness. For example, Niering

(1963) considered that increased soil maturity, soil moisture and protection from salt spray above a 1.4-ha threshold-size allowed a larger pool of plants to colonize islands. Wiens (1962) proposed that the threshold was connected to the development of a freshwater lens on reef islands. Similarly, Whitehead & Jones (1969) studying the plants of Kapingamarangi Atoll, argued that very small islands, smaller than 100 m² of area, are covered completely by strandline habitats and therefore their flora is composed of species that generally do not respond to small variations in the area. Whitehead & Jones (1969) then argue that as islands get larger, new habitats are added (e.g. atolls with a freshwater lens have habitats free of salt water). Accordingly, Triantis *et al.* (2006) described the SIE as an idiosyncratic phenomenon, independent from the direct effects of area, and mainly driven by the effects of habitat diversity.

The second group of explanations has its roots in MacArthur & Wilson (1967; p. 30), who suggested that for small, unstable islands, extinction rates may be area-independent. Small islands are subject to episodic instability and catastrophic events, such as inundation by tidal surges or devastation by storms, which may lead to total extinction of plants, keeping the islands below equilibrium levels. Community instability on a small island has been documented in a series of detailed censuses by Heatwole & Levins (1973), who showed high immigration and extinction rates and rapid species turnover. They attributed the extinction of species to unsuitable climatic and habitat characteristics, erosion due to waves, and hurricane damage to vegetation and to the island itself. Schoener *et al.* (2001) came to similar results, with altitude being more important than area in determining on which islands individuals are not drowned or washed away by sudden inundating rise in sea level caused by hurricanes, although subsequent recovery relates to area.

Hence, the explanation of SIE has been connected to demographic stochasticity (i.e. extinction rates independent of island area – MacArthur & Wilson, 1967), and with idiosyncratic habitat diversity at small spatial scales (Triantis *et al.*, 2006). These two explanations offer contrasting predictions of which species occur on small islands. First, habitat diversity argues that species on small islands should be disproportionately habitat generalists, with habitat specialists occurring irregularly according to the idiosyncratic habitat features of each island. Demographic stochasticity alone should not lead to a different representation of generalists and specialists, unless habitat range exploitation affects population size, in which case generalists would have larger populations, as they exploit a wider range of local habitats, so demographic stochasticity would affect generalists more mildly than specialists.

From the point of view of species presence–absence patterns, the SIE is evidently related to the minimum area of species occurrences. The diversity-related patterns of species occurrences on islands have been described by incidence functions (Diamond, 1975). At the same time, the area-related ‘incidence functions’ have not been addressed accordingly (but see Watson *et al.*, 2005), despite the fact that such incidence functions would be directly related to the SIE, since small island communities are formed in response to the minimum area requirements of species

constituting the overall available pool. The concept of minimum area requirements for animal and plant species has been addressed mainly as a species-specific population biology issue, even though it is highly relevant also for community assembly and island biogeography theory.

A systematic investigation of SIE asks for a serious consideration of habitat diversity as a causal factor of species richness. The term ‘habitat diversity’ has been used more or less inconsistently in the ecological literature (see Looijen, 1998), but most authors use it to express the environmental heterogeneity experienced by the organisms under study. In addition, the measurement of habitat diversity poses some important methodological issues too (Triantis *et al.*, 2003, 2005). Herein, we adopt a taxon-specific approach to habitat diversity, which we consider more suitable for the exploration of SIE.

In this paper we examine the terrestrial isopod fauna of Aegean islands to assess the importance of habitat diversity and demographic stochasticity on the structure of small island communities.

METHODS

For the purposes of the present analysis, we assembled a data matrix consisting of the distribution of 85 terrestrial isopod species on 90 Aegean islands (Table 1) ranging from 0.0023 to 8261 km² in size, adapted from Sfenthourakis (1994, 1996a), Schmalfuss *et al.* (2004) and Triantis *et al.* (2008). After the exclusion of halophilous species (see below), 76 species were included in the present work.

Three methods have been proposed so far for the identification of SIEs. Lomolino & Weiser (2001) used a recursive regression function, both in its semilog and log-log form, in search of a breakpoint below which there is no significant species–area relationship. Gentile & Argano (2005) used a similar approach, differing in that the threshold in their equation corresponds to a breakpoint dividing the overall species–area regression line into two lines with different slopes. Triantis *et al.* (2006) used path analysis to account for the separate and combined effects of area and habitat diversity on species richness. A SIE is recognized at a threshold below which the direct effects of area become insignificant. Of these three methods, only the one of Triantis *et al.* (2006) explicitly incorporates habitat diversity.

Habitat diversity of all islands was estimated following Sfenthourakis (1994, 1996b), using aspects of the environment known to be important to the ecological requirements of terrestrial isopods. A total of 16 habitat types were identified (Table 2), 14 recognized by Sfenthourakis (1994) for central Aegean islands plus two more for Crete so as to include habitats present on high mountains, i.e. highlands with arboreal/shrubby vegetation, highland/subalpine rocky outcrops with herbaceous plants. All the habitat types are structured as special habitats within more general habitat type groups.

Species were assigned as generalists or specialists according to how many different habitat type groups they exploit. Species that occupied only one habitat type group were considered specialists. Species that occupied more than one habitat type group were

Table 1 The islands studied in this work with their respective area (A), altitude (Alt), total numbers of habitats (H) (excluding coastal habitat types), total species richness (S) (after the exclusion of halophilous species), ratios of specialist to generalist species (s/g), cumulative ratios of specialist to generalist species for islands ranked according to increasing area (s/g cumA), altitude (s/g cumAlt), habitat diversity (s/g cumH).

Island name	A (km ²)	Alt (m)	H	S	s/g	s/g cumA	s/g cumAlt	s/g cumH
Crete	8261.1830	2456	16	34	0.700	1.235	1.235	1.235
Samos	477.9420	1160	14	29	0.450	1.121	1.121	1.121
Naxos	389.4340	1002	13	32	0.600	1.121	1.121	1.121
Andros	383.0220	994	13	26	0.444	1.091	1.091	1.091
Kos	287.6110	846	12	29	0.450	1.061	1.030	1.030
Ikaria	255.3200	1005	14	26	0.300	1.031	1.121	1.121
Tinos	197.0440	725	12	24	0.333	0.969	0.969	0.969
Paros	196.7550	706	10	18	0.200	0.938	0.937	0.903
Milos	158.4030	751	9	21	0.313	0.938	0.969	0.806
Kea	131.6930	547	12	20	0.250	0.938	0.844	0.938
Amorgos	121.4640	821	10	23	0.278	0.906	0.969	0.903
Kalymnos	110.5810	676	7	17	0.417	0.875	0.875	0.733
Kythnos	99.4320	255	11	16	0.231	0.875	0.654	0.906
Astypalaia	96.4200	482	10	19	0.188	0.871	0.812	0.871
Mykonos	86.1250	372	8	15	0	0.871	0.677	0.742
Syros	84.0690	442	11	20	0.250	0.871	0.781	0.935
Sifnos	77.3710	678	11	21	0.167	0.806	0.875	0.903
Thira	76.1940	564	8	14	0.273	0.774	0.844	0.767
Serifos	74.3310	582	9	20	0.250	0.774	0.844	0.774
Kasos	66.4190	601	8	18	0.200	0.774	0.875	0.767
Leros	54.0520	321	10	18	0.286	0.742	0.677	0.839
Nisyros	41.2630	698	9	20	0.333	0.733	0.906	0.774
Anafi	38.6360	579	7	15	0.154	0.700	0.844	0.633
Antiparos	35.0900	300	7	14	0.273	0.700	0.667	0.655
Patmos	34.1420	272	8	18	0.385	0.700	0.714	0.733
Antikythira	19.6785	378	6	14	0.400	0.679	0.719	0.643
Pserimos	14.6300	265	7	11	0.100	0.630	0.654	0.679
Dia	11.8802	268	3	8	0.333	0.630	0.692	0.273
Levitha	9.1210	130	7	14	0.400	0.593	0.500	0.679
Antimilos	8.2000	671	2	7	0	0.556	0.875	0.118
Telendos	4.6500	460	6	8	0.333	0.556	0.812	0.593
Kinaros	4.5770	296	4	11	0.222	0.519	0.667	0.500
Gyali	4.5580	459	6	9	0.125	0.538	0.781	0.556
Dilos	3.4000	112	4	6	0	0.538	0.375	0.520
Stouronisi (Evvoia)	3.0500	165	4	9	0.286	0.538	0.480	0.520
Armathia (Kasos)	2.5670	106	4	12	0.333	0.560	0.375	0.542
Ofidousa (Astypalaia)	1.9120	122	5	9	0.286	0.480	0.417	0.577
Velopoula (Milos)	1.8080	227	4	5	0.250	0.480	0.600	0.458
Pacheia (Anafi)	1.4800	229	3	5	0.250	0.440	0.600	0.227
Kounoupoi (Astypalaia)	1.4450	87	6	8	0.143	0.440	0.167	0.556
Kandelioussa (Nisyros)	1.3640	103	4	7	0.400	0.440	0.250	0.417
Falkonera (Milos)	1.2900	218	3	4	0.333	0.360	0.560	0.227
Christiani (Thira)	1.2100	285	4	5	0	0.320	0.690	0.333
Pergousa (Nisyros)	1.2000	81	4	8	0	0.333	0.182	0.333
Anydros (Anafi)	1.1300	194	4	8	0.600	0.348	0.520	0.364
Pacheia (Nisyros)	1.0000	137	3	3	0	0.261	0.500	0.182
Pontikoussa (Astypalaia)	0.9700	224	5	6	0.500	0.261	0.560	0.577
Agria Gramvousa (Crete)	0.7987	100	3	5	0	0.217	0.167	0.182
Plati (Kalymnos)	0.7200	48	5	6	0	0.217	0.158	0.538
Paximadi (W) (Crete)	0.7142	252	2	2	0	0.217	0.600	0.125
Paximadi (E) (Crete)	0.5964	166	2	2	0	0.217	0.480	0.125
Fokionisi-large (Astypalaia)	0.5700	48	2	5	0	0.217	0.167	0.125
Makra (Anafi)	0.5600	124	2	2	0	0.217	0.417	0.125
Nera (Kalymnos)	0.5000	60	5	5	0	0.217	0.190	0.538

Table 1 *Continued*

Island name	A (km ²)	Alt (m)	H	S	s/g	s/g cumA	s/g cumAlt	s/g cumH
Koutsomytis (Astypalaia)	0.4700	55	6	8	0.143	0.217	0.200	0.556
Chondros (Astypalaia)	0.3850	88	5	6	0.200	0.238	0.167	0.538
Prasonisi (Antikythira)	0.3506	129	3	8	0.333	0.190	0.458	0.182
Makra (Kasos)	0.3086	124	3	5	0	0.143	0.417	0.136
Kalavros (Kalymnos)	0.2800	87	4	7	0	0.143	0.167	0.273
Pontikonisi (Crete)	0.2777	168	3	1	0	0.143	0.480	0.136
Agia Kyriaki (Astypalaia)	0.2550	21	2	4	0	0.143	0.077	0.125
Askania (Thira)	0.2500	171	3	4	0	0.143	0.480	0.136
Lianos (Astypalaia)	0.2350	28	4	6	0	0.143	0.058	0.273
Petousi (Evvoia)	0.1508	29	3	5	0	0.143	0.059	0.136
Agia Kyriaki (Kalymnos)	0.1500	55	3	3	0	0.143	0.158	0.136
Safonidi (Kalymnos)	0.1500	8	3	3	0	0.143	0	0.136
Ananes (Milos)	0.1000	82	3	5	0	0.143	0.167	0.136
Parthenopi (Evvoia)	0.0975	81	3	7	0	0.158	0.190	0.150
Fokionisi-small (Astypalaia)	0.0898	44	2	3	0	0.176	0.167	0.125
Tigani (Astypalaia)	0.0748	27	2	5	0	0.176	0.062	0.125
Agios Andreas (Evvoia)	0.0663	34	3	7	0.167	0.188	0.118	0.167
Fteno-large (Anafi)	0.0550	17	2	4	0.333	0.125	0.077	0.133
Fonias (Evvoia)	0.0525	26	3	5	0	0.063	0.067	0.111
Mavri (W) (Levitha)	0.0500	52	1	2	0	0.067	0.158	0.000
Mavri (E) (Levitha)	0.0500	40	1	2	0	0.067	0.118	0.000
Lytra (Kasos)	0.0485	25	2	4	0	0.067	0.071	0.067
Platourada (Evvoia)	0.0474	15	1	4	0	0.067	0	0.000
Avgo (Crete)	0.0433	52	1	2	0	0.071	0.158	0.000
Tigani (Evvoia)	0.0391	10	2	2	0	0.071	0	0.067
Lagouvardos (Antikythira)	0.0354	42	2	5	0.250	0.071	0.167	0.067
Karofyla (Kasos)	0.0315	20	1	2	0	0.000	0.077	0.000
Kouneli-large (Evvoia)	0.0307	29	1	4	0	0.000	0.059	0.000
Sari (Kalymnos)	0.0300	25	2	3	0	0.000	0.071	0.000
Agios Andreas (Kalymnos)	0.0300	27	2	4	0	0.000	0.067	0.000
Fteno-small (Anafi)	0.0250	15	1	3	0	0.000	0	0.000
Fteno (Astypalaia)	0.0194	17	2	4	0	0.000	0	0.000
Nekrothiki (Astypalaia)	0.0100	5	1	2	0	0.000	0	0.000
Kouneli-small (Evvoia)	0.0077	8	1	3	0	0.000	0	0.000
Krevvati (Kalymnos)	0.0040	2	1	3	0	0.000	0	0.000
Diapori (Astypalaia)	0.0023	3	1	2	0	0.000	0	0.000

considered generalists. Obviously, the use of only two categories is a simplification, considering the continuum between strict specialists and broad generalists, but we considered this approach more useful for the sake of clarity and generality.

Halophilous species (and corresponding habitat types, e.g. sand beaches, rocky shores, etc.) were excluded from the analyses for two reasons. First, their records could be incomplete due to the fact that large parts of the rocky shores are almost inaccessible to researchers, and second, because issues related to insular habitat diversity can be explored in a more meaningful way when purely terrestrial habitats are considered. In fact, the occurrence of halophilous species on islands of any size is not particularly informative, since all islands have almost the same suite of coastal habitats regardless of their size (Sfenthourakis, 1996a).

For each species, the minimum island area and the island area range (maximum minus minimum area) of actual occurrences

were recorded. The ratios of specialists to generalists were calculated for each individual island and for the cumulative values for islands arranged according to increasing area, altitude and habitat diversity. The relationships of the per island ratio of specialists to generalists with island area, altitude and habitat diversity were examined using linear regressions for each independent factor separately and stepwise multiple regression for all the three factors.

We used chi-square tests (with Yate's correction) for each separate island in order to test if the cumulative ratios of specialists to generalists when islands are arranged according to area, habitat diversity and altitude differ from the ratio of the overall data set. Linear regressions of these ratios to area, altitude and habitat diversity were also applied. We additionally calculated the correlations among the three predictor variables, i.e. area, altitude and habitat diversity, to check for possible confounding effects due to collinearity.

Table 2 The habitat types recognized for the purposes of the present study, classified in general habitat type groups.

Habitat type group	Habitat types
A:	(1) Salt marshes/mudflats
B:	(2) Phrygana (seasonal dwarf-shrubs, Mediterranean heaths)
C: Maquis (Mediterranean evergreen sclerophyllous shrubs):	(3) Degraded dry maquis (4) Dense humid maquis
D: Stands of arboreal vegetation:	(5) Coniferous stands (6) Broad-leaved trees
E: Cultivated land:	(7) Olive groves (8) Fruit-bearing trees (9) Herbaceous plants
F: Riparian habitats:	(10) Stream/river banks with dense arboreal vegetation (11) Stream/river banks with shrubby hygrophilous plants (12) Dry stream banks without hygrophilous vegetation
G:	(13) Bare rocks with very sparse plant or soil cover
H:	(14) Human settlements
I: Highland/subalpine sites (only on Crete):	(15) Highlands with arboreal/shrubby vegetation (16) Highland/subalpine rocky outcrops with herbaceous plants

Table 3 The upper limits of the Small Island Effect (SIE) detected by the two models, since the method of Gentile & Argano (2005) did not detect a SIE, the numbers of islands included within the SIE range, the numbers of specialist (s) and generalist (g) species present on islands within and outside the SIE range, and the results of the chi-square tests (with Yates' correction) for the comparison of the s/g ratios between these two groups of islands, with their corresponding probability level (*P*).

	SIE upper limit (km ²)	Islands within SIE	Species on islands within SIE		Species on islands outside SIE		Chi-square	<i>P</i>
			s	g	s	g		
Triantis <i>et al.</i> (2006)	4.558	58	14	26	38	34	2.59	0.10
Lomolino & Weiser (2001)	1	45	6	23	42	34	8.77	0.003

We tested for differences between generalists and specialists in minimum island area (MA) and area range (AR) using one-way ANOVA. We used chi-square tests (with Yate's correction) for differences in the presence of generalists and specialists on islands above and below the SIE threshold.

RESULTS

Among the 76 species present in the studied islands, 34 are generalists and 42 are specialists. Generalists show no difference in MA ($F = 2.43, P > 0.05$) but a higher island AR than specialists ($F = 11.56, P < 0.002$). There is also a significant difference between the number of islands occupied by generalists and specialists ($F = 33.6, P < 0.001$, mean generalists: 21 ± 3 , mean specialists: 4 ± 1).

A significant SIE was detected by two of the three methods. The estimated range of the SIE differs between the two methods that detected a significant SIE, being 1 km² for the method of Lomolino & Weiser (2001) using the semilog function, and 4.558 km² for that of Triantis *et al.* (2006). No significant SIE was found by the method of Gentile & Argano (2005). The upper

limits of the SIE, the number of islands included within the SIE range and the numbers of specialist and generalist species occurring on islands within and outside the SIE range for the two methods that detected a significant SIE are given in Table 3. The number of habitats and area (log-transformed values) were highly correlated for the entire data set ($R^2 = 0.84, P < 0.001$) as well as below the SIE threshold ($R^2 = 0.63, P < 0.001$ for the threshold estimated following Triantis *et al.*, 2006; $R^2 = 0.54, P < 0.001$ for the threshold from Lomolino & Weiser, 2001). The relationship becomes statistically insignificant only for islands smaller than 0.05 km². The percentage of species richness' variance explained by area, by habitats and by altitude for all islands and the islands within and outside the SIE range as estimated according to the methods of Triantis *et al.* (2006) and Lomolino & Weiser (2001) is given in Table 4.

The specialists to generalists ratios differed significantly between the islands included in the SIE and those not included for the method of Lomolino & Weiser (2001), but only marginally ($P = 0.10$) for the method of Triantis *et al.* (2006). Small islands had lower specialists:generalists ratios than large islands (Table 3). Specialists to generalists ratios were linearly related to

Variable	All islands	Triantis <i>et al.</i> (2006)		Lomolino & Weiser (2001)	
		Within SIE	Outside SIE	Within SIE	Outside SIE
Area	0.79**	0.28**	0.76**	0.09*	0.84**
Habitats	0.81**	0.48**	0.81**	0.35**	0.83**
Altitude	0.59**	0.15*	0.37**	ns	0.54**

island area ($R^2 = 0.463$, $P < 0.001$) and habitat diversity ($R^2 = 0.441$, $P < 0.001$), but only area enters in the multiple regression model ($R^2 = 0.500$, $P < 0.001$). The relationship with area is not significant below an area of 1.15 km^2 (45 islands).

The cumulative ratios of specialists to generalists (see Table 1) for islands arranged according to area is significantly different (chi-square test, $P < 0.05$) from the overall ratio up to the area of 4.577 km^2 , for islands arranged according to altitude, below around 171 m a.s.l. , while for islands arranged according to habitat diversity till islands with four habitat types. The three variables, nevertheless, are significantly intercorrelated (area–altitude $r = 0.92$, $P < 0.001$; area–habitat diversity $r = 0.91$, $P < 0.001$; altitude–habitat diversity $r = 0.79$, $P < 0.001$). In view of this collinearity, islands below the three thresholds have an area of less than 4.577 km^2 , except for Dia, which is exceptionally poor in habitat diversity for its size, and Levitha for altitude (which is quite low for its size and habitat diversity).

Cumulative ratios of specialists to generalists are linearly related with log-area, log-altitude and habitat diversity (Fig. 1). This means that the frequency of specialists is consistently increasing in relation to generalists with area, altitude and habitat diversity.

The ratio of generalists to specialists with a MA within the SIE limits (26/14) is significantly larger than the respective ratio (8/28) outside these limits ($\chi^2 = 12.35$, $P < 0.001$). This means that there are more generalist species for which the minimum area of occurrence falls within the SIE limits, whereas most specialists stop being present in a MA outside these limits. At the upper SIE threshold, two-thirds of specialists, but only a quarter of generalists, have reached their MA. This pattern is graphically depicted in Figs 2 and 3. Figure 2 shows the ratio of generalists to specialists with a MA on each island in relation to island area, a ratio that consistently falls with increasing area. Figure 3 shows the percentages of specialists and generalists with a MA in each island (or larger) to the total number of specialists and generalists, respectively, in relation to island area. It is evident that the ratio of generalists falls more rapidly (i.e. on smaller islands) than the one of specialists, showing that more specialists have their MA on larger islands.

DISCUSSION

A SIE for the terrestrial isopods of 90 Aegean islands was detected by two of the three methods applied herein, i.e. Lomolino & Weiser (2001) and Triantis *et al.* (2006). The estimated range of the SIE differs between the two methods, being 1 km^2 for the

Table 4 The coefficient of determination (R^2) of the relationships between area, habitats and altitude with species richness for all islands, and for islands within and outside the Small Island Effect (SIE) range according to two models. *: $P < 0.05$, **: $P < 0.001$, ns: non-significant.

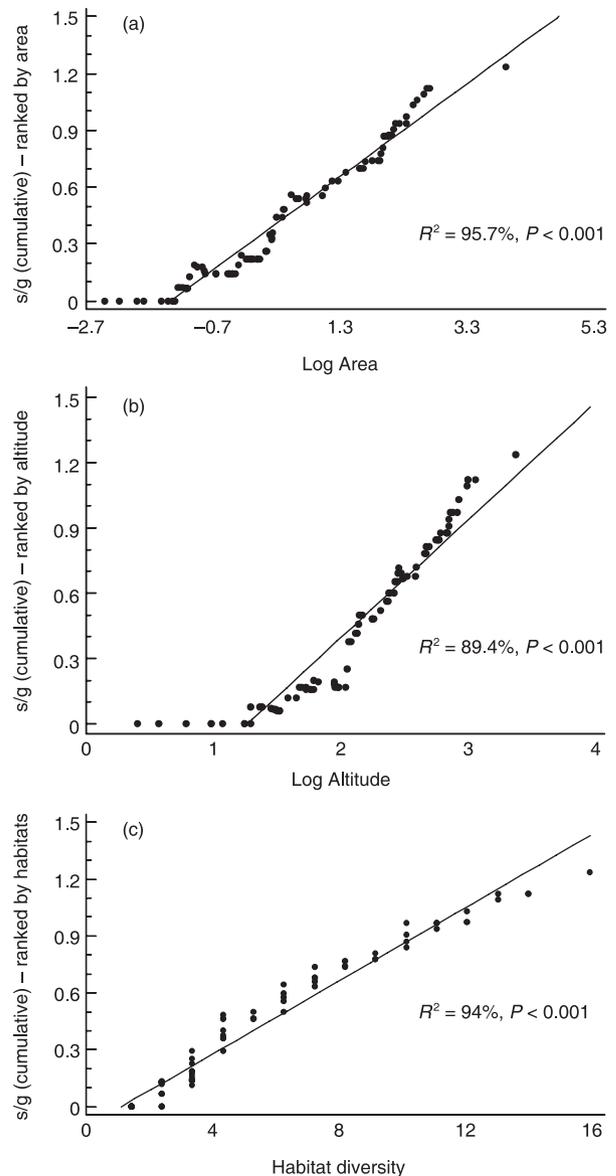


Figure 1 The relationship of the cumulative ratio of specialists to generalists (s/g-cumulative) for islands ranked by area, altitude and habitat diversity with area (a), altitude (b) and habitat diversity (c), respectively.

method of Lomolino & Weiser (2001) and 4.558 km^2 for that of Triantis *et al.* (2006). Gentile & Argano (2005) had detected a significant SIE in a subset of the present data set containing 43 Aegean islands with their method (0.501 km^2) but for the current

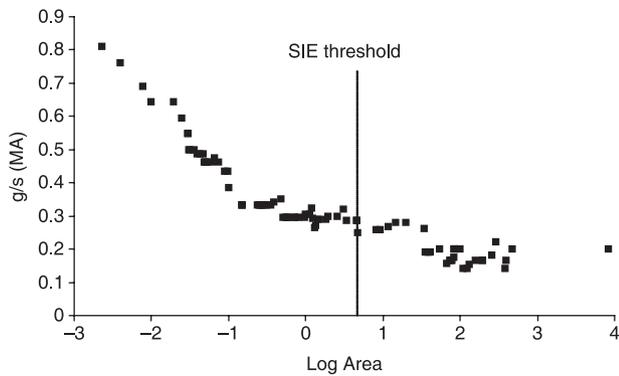


Figure 2 The ratio of generalists to specialists with a minimum area ($g/s(MA)$) of occurrence on each island, in relation to the respective area of each island. The Small Island Effect (SIE) threshold according to the method of Triantis *et al.* (2006) is shown.

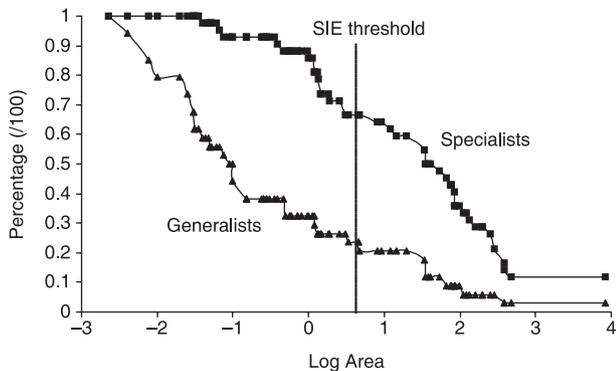


Figure 3 The percentages of species (divided in specialists and generalists) with a minimum area (MA) at each island (or larger) to the total numbers of species (specialists or generalists, respectively), in relation to the area of each island. The Small Island Effect (SIE) threshold according to the method of Triantis *et al.* (2006) is shown.

data set their method is not detecting the phenomenon. This discrepancy of results might be an indication that methods solely based on area measurements are sensitive to the actual distribution of area values used in each study. The variation in the results among the three methods can be assigned to their differences in how the area effects are assessed and to the consideration of habitat diversity (see Triantis *et al.*, 2006, 2008). It is clear that strong collinearity among area and habitat diversity in the present data set is an important confounding factor for the explanation of Aegean isopod species richness. Thus, we consider the method of Triantis *et al.* (2006), which decouples the effects of area and habitat diversity through path analysis and is also independent from the classical species–area relationships, as more robust, at least for this data set. The convergence of the SIE value found by this method (4.558 km^2) with the island size where the cumulative ratio of specialists to generalists diverges from that of the overall data set (4.577 km^2), strengthens our appreciation of its merits.

Due to the complexity of these tripartite interactions in ecological systems, the estimated upper limits of the SIE are not strict boundaries but approximations of the critical range of island areas where the general pattern is changing ‘behaviour’. For example Triantis *et al.* (2006) report an upper SIE limit at 3.4 km^2 for terrestrial isopods in the above mentioned subset of the present data set consisting of 43 islands. Thus, the convergence of this value with the one estimated by the present work, at around $3\text{--}5 \text{ km}^2$, indicates that islands near and below this size class are mostly under the effect of habitat diversity, as mediated also through indirect area effects. We cannot exclude a role of other factors, such as current or past island isolation, which are not easily quantified for these islands because of the complex topography and palaeogeographical history of the area (see Triantis *et al.*, 2005, 2006).

In the present data set, there is a strong correlation between species richness and habitat diversity, and habitat diversity and area throughout the range of areas larger than 0.05 km^2 . The strong correlation of area and habitat diversity likely results from the interdependence of area and the presence of specific habitat types (Kohn & Walsh, 1994; Triantis *et al.*, 2005). Certain habitat types occur only on the larger islands, such as small streams and habitats associated with anthropogenic biotopes (e.g. cultivation, settlements) (Sfenthourakis, 1996b). Nevertheless, the relationship between the numbers of habitats with area within the limits of the SIE is weakened compared to the same relationship for all islands. In general, for larger islands habitat diversity is increasing with the increase of area in a quite predictable fashion when on smaller islands the relationship is becoming more fluctuant. On larger islands, the increased habitat diversity, arising from greater topographical and geological heterogeneity, is promoting increased species richness, particularly when the species involved tend to be habitat specialists (Hart & Horwitz, 1991; Ricklefs & Lovette, 1999; Whittaker & Fernández-Palacios, 2007).

The SIE is present when area does not influence species richness directly, whereas indirect effects may still be present (Triantis *et al.*, 2006). The direct effects of area are mediated either by the larger target for dispersing individuals offered by larger islands, or by the larger populations that larger islands can support (Lomolino, 1990; Ricklefs & Lovette, 1999; Whittaker & Fernández-Palacios, 2007). We can assume that ‘target effects’ should play a role mainly for active or airborne disperses, while for taxa like terrestrial isopods they would be negligible (see also Triantis *et al.*, 2008). Furthermore, the effect of area on population size is also taxon-specific, since species of small-sized animals can maintain viable populations even in really small areas, if their habitat requirements are satisfied. This is expected to happen more often for generalist species.

It has become evident that generalist species dominate the isopod fauna of islands within the limits of the SIE. As expected, generalists exploit a wider range of island sizes than specialists, even though the minimum area of occurrence does not differ between these groups. The latter should be assigned to the fact that there are several specialists that can be found in a few small islands depending on their idiosyncratic habitat structure and because many small islands of the Aegean behave as parts of their

neighbouring larger islands (see Triantis & Mylonas, 2008). The contribution of specialists to isopod communities increases with area, altitude and habitat diversity, and there are certain thresholds of all these factors above which the ratio of specialists to generalists does not differ from the overall ratio. Given the intercorrelation among area, altitude and habitat diversity, we may assume that there is a certain island 'configuration' that represents the point of shift in isopod community structure in terms of specialist and generalist species. This threshold can be identified quite accurately by any of these variables, and has been approximated very closely by the SIE threshold identified by the method of Triantis *et al.* (2006). Thus, a representative sample of the overall species list of the archipelago is attained when islands larger than 4.6 km², having a maximum elevation higher than 170 m and hosting more than four habitat types, are included in the data set. Below this threshold, the communities are biased towards generalists, a pattern evidently contributing to the resulting 'anomalous' behaviour of small islands.

The present analysis revealed that there is a core group of species occurring on small islands, with a high degree of predictability. According to Sfenthourakis (1996a) and Gentile & Argano (2005), the isopod fauna of small islands is dominated by common species with broader distributions than those of larger islands. Species with broader occurrence are mostly generalists, as can be seen in Fig. 4. The species comprising the core group are

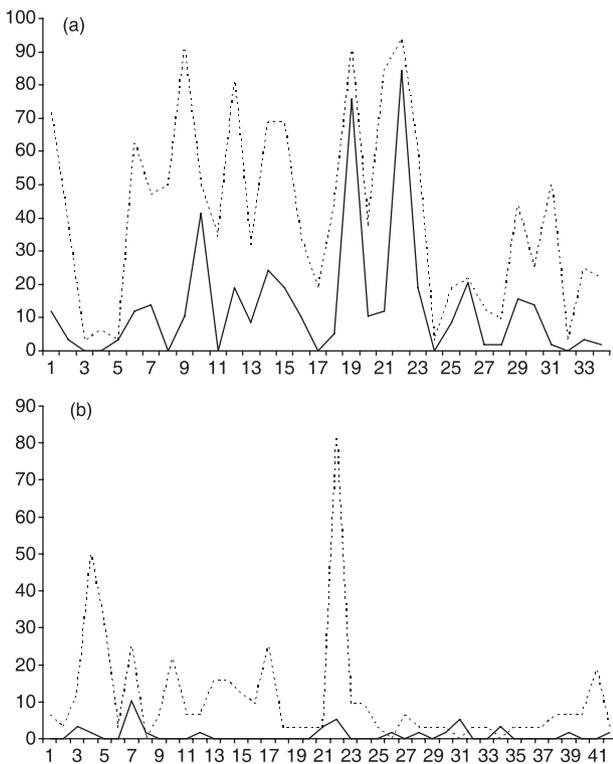


Figure 4 Percentage of islands occupied by (a) generalist and (b) specialist species (horizontal axis, numbers stand for individual species). Islands inside Small Island Effect (SIE) (solid lines) and outside SIE (dashed lines).

widespread generalists such as *Porcellionides pruinosus*, *Platyarthrus schoebli* and *Armadillo tuberculatus*. Species occurring on more than three islands (so that their patterns of occurrence can be meaningfully evaluated from an ecological perspective), whose minimum area of occurrence is outside the maximum SIE range, are: *Ligidium cycladicum*, *L. ghigii*, *Trichoniscus rhodiensis*, *Graeconiscus thermophilus*, *Chaetophiloscia elongata*, *Nagurus aegaeus*, *Leptotrichus syrensis* (specialists), *Trichoniscus pygmaeus*, *Bathytropa granulata*, *Platyarthrus beieri*, and *Armadillidium vulgare* (generalists). In addition, the minimum area of occurrence of the species *Trachelipus aegaeus*, *Armadillidium ameglioii*, *A. marmoratum* (specialists), *Agabiformius obtusus*, *Porcellio laevis* and *Schizidium aegaeum* (generalists) lies within the 'ambiguity range' for the upper limit of the SIE as estimated by the two models. Finally, *Trichoniscus oedipus* and *Schizidium album* (generalists) are only present in just one island inside the SIE range, while they are present mainly on larger islands. More than half of these (11 out of 19) are species depending on freshwater habitats, being either strictly riparian or living in soaked substrate such as in the small marshes often formed at low flat sites just behind the coastal zone. Three more are found only in very humid plant litter layer and two more are endogean species found only in sites with very wet soil. The habitat requirements of the remaining three species are not clear. It should be noted also that the majority of species with three or less occurrences are also either riparian or endogean living in soaked soil. These observations stress the importance of water-related habitat types for terrestrial isopod diversity. Indeed, these kinds of habitats are absent from the vast majority of small islands in the Aegean Sea.

Another crucial factor is calcareous substrate, whose presence should be considered as a limiting factor for the following species: *Porcellio flavomarginatus*, *P. wernerii*, *Echinarmadillidium* spp., *Armadillidium ameglioii* and *Armadillo tuberculatus* (Sfenthourakis, 1994). Most of these species occur in a wide range of island areas due to the fact that limestone is the most common geological substrate throughout the region.

The finding of Sfenthourakis *et al.* (2004) that Aegean terrestrial isopods cannot be locally rare and geographically common but can be locally common and geographically rare adds further support to the significance of the distribution of critical habitat types for the distributional patterns of these animals. Even though terrestrial isopods, as a group, are considered hygrophilous, at a local scale they are represented by a wide range of ecological forms, exploiting almost all available habitats. In the Aegean region, there are even specialists that are restricted to dry habitats, like calcareous rocky substrate (e.g. *Porcellio wernerii*, *Echinarmadillium* spp.). Nevertheless, water-related habitats are crucial for their overall diversity, since more than 50% of specialist species are related with the particular habitat type, 23 of 42 specialists are species found only at such habitats, and 10 more are endogean species found only in very humid soil. The complete absence of specialists from the large islands of Mykonos (86 km²) and Anafi (39 km²) is indicative of the whole pattern, as they are among the driest in the Aegean.

The increased importance of habitat diversity for specialists, in contrast to generalists that are mostly affected by area, has been

shown also by Azeria (2004) for vertebrates in the Dahlak archipelago (Red Sea). This is mainly due to the fact that, as Norris & Harper (2004) argue, habitat specialists are expected to cope less well with environmental change compared with generalists, since they cannot persist if their limited habitat is destroyed.

The water-related habitats correspond to the 'keystone structures' recognized by Tews *et al.* (2004), although these authors discriminate between keystone habitats and keystone structures. Inland water-related habitats are not a habitat type in the traditional sense, but rather a group of habitat types that share the presence of an almost saturated humid microenvironment. In this sense, they may be regarded as a 'keystone structure'. As such, they are of prime importance for the conservation of isopod diversity on Aegean, and more generally, Mediterranean islands. These freshwater-related habitats are among the most vulnerable ecosystems of Aegean islands, due to the ongoing depletion of water resources, mainly due to the development of tourism and/or climate change. The insular inland waters act as refuges for most hydrophilic species and host high levels of diversity within very restricted areas, but are vulnerable to human intrusion and encroachment: they are drained, deprived of their crucial freshwater inputs, overpumped, overgrazed, dumped, split by roads, polluted by sewage, filled with rubble, cultivated or turned into airports (Catsadorakis & Paragamian, 2007). The reduction of wetlands on the Aegean islands will drive to extinction many species dependent on them but will also result in a significant reduction of the stop-over sites of millions of migrant birds (Triantis & Mylonas, 2008).

In more general terms, the present work highlights the crucial role of habitat type distribution and diversity for the presence of a significant SIE, despite an apparent strong species–area relationship at all size scales. In its original interpretation, the SIE was defined as the prevalence of other factors than area in the determination of species richness. One such factor, possibly one of the most important, is the lack of crucial habitats (or keystone structures) below a certain area threshold. This threshold should vary among taxa, depending on their particular ecological requirements, but also for the same taxon on different archipelagos, depending on the local distribution and types of habitats. For example, no SIE was detected for plants on Aegean islets (Panitsa *et al.*, 2006), as well as for several other data sets for a variety of taxa (see Triantis *et al.*, 2006).

The simple methodological framework presented herein is directly applicable to any island group and to any taxon. Researchers with finer data on habitat preferences and/or niche breadth of the organisms under study can proceed to a more elaborate separation of species into categories, including intermediates between specialists and generalists. Such an approach will test the generality of our results and provide further insight into the structuring of small island communities and the possible ways of protecting and conserving them. As Zimmerman & Bierregaard (1986) noted, the knowledge of the autecological requirements of species is critical for reserve design.

The identification of a sparse occurrence of specialists on islands within the SIE range may have important implications for

conservation efforts, especially if it is shown to be a general pattern among various taxa. Specialists are more vulnerable to environmental perturbation, being restricted to specific habitat types. These habitat types, in turn, appear at restricted number of sites on each island, usually correlated with its surface area, so that extinction probability of specialists on large islands is relatively lower than on small for reasons other than (or additional to) sustainable population size. As a consequence, given also that very small islands generally do not host specialists, we conclude that islands near the SIE threshold should be of special conservation concern, together with the 'keystone structures' identified in each case.

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