



# Island biogeography of the Mediterranean sea: the species–area relationship for terrestrial isopods

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## ABSTRACT

**Aim** We looked at the biogeographical patterns of Oniscidean fauna from the small islands of the Mediterranean Sea in order to investigate the species–area relationship and to test for area-range effects.

**Location** The Mediterranean Sea.

**Methods** We compiled from the literature a data set of 176 species of Oniscidea (terrestrial isopods) distributed over 124 Mediterranean islands. Jaccard’s index was used as input for a UPGMA cluster analysis. The species–area relationship was investigated by applying linear, semi-logarithmic, logarithmic and sigmoid models. We also investigated a possible ‘small island effect’ (SIE) by performing breakpoint regression. We used a cumulative and a sliding-window approach to evaluate scale-dependent area-range effects on the log *S*/log *A* regression parameters.

**Results** Based on similarity indexes, results indicated that small islands of the Mediterranean Sea can be divided into two major groups: eastern and western. In general, islands from eastern archipelagos were linked together at similarity values higher than those observed for western Mediterranean islands. This is consistent with a more even distribution of species in the eastern Mediterranean islands. Separate archipelagos in the western Mediterranean could be discriminated, with the exception of islets, which tended to group together at the lowest similarity values regardless of the archipelago to which they belong. Islets were characterized by a few common species with large ranges. The species–area logarithmic model did not always provide the best fit. Most continental archipelagos showed very similar intercepts, higher than the intercept for the Canary island oceanic archipelago. Sigmoid regression returned convex curves. Evidence for a SIE was found, whereas area-range effects that are dependent on larger scale analyses were not unambiguously supported.

**Main conclusions** The Oniscidea fauna from small islands of the Mediterranean Sea is highly structured, with major and minor geographical patterns being identifiable. Some but not all of the biogeographical complexity can be explained by interpreting the different shapes of species–area curves. Despite its flexibility, the sigmoid model tested did not always provide the best fit. Moreover, when the model did provide a good fit the curves looked convex, not sigmoid. We found evidence for a SIE, and minor support for scale-dependent area-range effects.

## Keywords

Breakpoint analysis, cluster analysis, island biogeography, isopods, Mediterranean, Oniscidea, similarity index, small island effect, species–area relationship.

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## INTRODUCTION

Of all the Crustaceans, the Oniscidea is undoubtedly the group that has been most successful in colonizing terrestrial environments. Although these isopods are found in a variety of different habitats, they are characterized by low dispersal ability and a high degree of stenocoecy. A combination of these characteristics is often a determinant of the high degree of morphological and/or genetic variation exhibited by species of this suborder over time and space, at both micro- and macro-scales (Gentile & Sbordoni, 1998; Sarbu *et al.*, 2000). 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; G. Gentile and R. Argano, unpubl. data). 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.

Many studies of the Oniscidea of Mediterranean islands have been carried out, primarily focusing on local faunas (Arcangeli, 1953; Ferrara & Taiti, 1978; Taiti & Ferrara, 1980, 1989; Caruso *et al.*, 1987; Argano & Manicastro, 1996; Sfenthourakis, 1996a,b; G. Gentile & R. Argano, unpubl. data). Up until now, with the exception of the work by Sfenthourakis (1996a,b), there has been little use made of the available data, despite their biogeographical relevance. In fact, these data could prove very useful, not only to investigate general biogeographical patterns of the Mediterranean area, but also to address the species–area issue, a topic of renewed interest among biogeographers.

In this study, numerical taxonomic techniques were applied to the data in order to perform an analysis of the Oniscidea fauna from a large sample of islands within the Mediterranean Sea. We use the species–area relationship to compare five continental archipelagos of the Mediterranean Sea and the oceanic archipelago of the Canary Islands. A range of linear and nonlinear models were used to verify the findings of Sfenthourakis (1996a), who investigated which model (linear, logarithmic or semi-logarithmic) should be applied to Oniscidea of the Canary, Aegean and Tuscanian islands. We also considered the biological relevance of the slope and intercept of the species–area relationship for Oniscidea of the islands of the Mediterranean Sea.

In general, estimates of slopes and intercepts can be affected by bias introduced by the area–range effect. Martin (1981) has shown that slope estimates may vary when the smallest and largest island ranges of some archipelagos are examined separately or cumulatively. In particular, he observed that slope estimates would be higher if based on ranges of small islands, whereas they would be lower when considering ranges of larger islands. Additionally, if the areas of two archipelagos overlap, but the range of one is extended to include larger or smaller islands, then the slope of the log  $S/\log A$  curve would be lower or higher respectively. The influence of spatial and

temporal scale on the nature of the species–area relationship, in relation to speciation, has been discussed by Lomolino (2000).

We also consider the ‘small island effect’ (SIE). The SIE refers to the existence of two different patterns in the species–area curve, whereas traditional models, such as the log  $S/\log A$  model, can usually describe only one pattern. The SIE shows that below a certain threshold value, the number of species can vary independently of area and that in this case, a sigmoid curve describes better the species–area relationship (Lomolino, 2000). To address this issue, Lomolino & Weiser (2001) used simple linear regression with a breakpoint transformation (McGee & Carleton, 1970; Besier & Sugihara, 1997). For the estimation of the breakpoint, which is the upper limit of the SIE, they used the equation:

$$\log S = b_0 + b_1[(\log A - T)(\log A \geq T)], \quad (\text{eqn 1})$$

where  $S$  and  $A$  are species richness and area respectively.  $T$  is the upper limit of the SIE and  $(\log A \geq T)$  is a logical variable that returns 1 or 0 if true or false respectively. Parameters of the equations were estimated by iteration, with  $T$  (in units of log  $A$ ) being incremented at each iteration. In this equation,  $x$ -values of islands smaller than  $T$  are reduced to 0, whereas  $x$ -values of islands larger or equal to  $T$  are decreased by the amount  $T$ .

With respect to the traditional models, the equation proposed by Lomolino & Weiser (2001) has the advantage that it describes in more detail the species–area relationship when a SIE exists. However, the equation is not very appropriate to assess whether or not a SIE exists in a certain data set because it *a priori* assumes a SIE and imposes it on the model. In fact,  $x$ -values are reduced to 0 when islands are smaller than  $T$  so that log  $S$  is estimated as a constant ( $b_0$ ).

We used our data to compare slopes and intercepts for six archipelagos that differ in island size. We also investigated the possible occurrence of the SIE on the shape of the species–area curve by using both the model proposed by Lomolino & Weiser (2001) and a more general model of piecewise regression that does not assume *a priori* the existence of a SIE. Lastly, we investigated the possible occurrence of an area effect, as reported by Martin (1981), by estimating determination coefficients ( $R^2$ ), slopes ( $z$ ) and intercepts ( $k$ ) by both adding islands of increasing/decreasing size, and using sliding-windows that encompassed islands of increasing size. Although the SIE effect exists in nature, it is still debated how common it is (Lomolino, 2000, 2002; Williamson *et al.*, 2001; Barrett *et al.*, 2003). In this regard, the inclusion of a disproportionately high number of large islands in biogeographical surveys could be one of the reasons why many studies failed to detect the effect (Lomolino, 2000; Lomolino & Weiser, 2001). In the present study, the island size distributions for each archipelago always showed a leptokurtic, right-skewed pattern, thus removing this bias.

Additionally, to gather more information from the data, we looked for possible covariation patterns between regression parameters and area distribution skewness, when

the area-range effect was investigated. Thus, at each step in the cumulative and sliding-window analyses the skewness of the area distribution was also calculated.

## METHODS

### Data set

Data for this study have been obtained from the literature. Additions and corrections have been performed whenever possible based on new data and personal communications. Although we have reviewed the specialized literature critically, these data could still suffer from an uneven sampling bias especially with respect to the inclusion or exclusion of troglobitic species, which are very narrowly distributed and are often limited to only a few islands. However, we are confident that the errors involved are small. Indeed, the presence/absence of these species from the data set did not seriously affect the estimation of  $z$  and  $k$  parameters, as shown in a test for the Sardinian islands ( $z = 0.227$ ,  $k = 1.052$  and  $z = 0.221$ ,  $k = 1.029$  when troglobitic species were included or removed respectively).

The Oniscidean data collected for analysis comprised 176 species and 124 islands from the Mediterranean Sea. Our data set comprises islands that range in area from small to relatively large, but does not include major Mediterranean islands such as Sardinia, Sicily, Corsica, Crete and Cyprus. Islands with areas around  $0.1 \text{ km}^2$  or smaller (22.3%) are defined as islets, whereas the term 'small islands' refers to islands with areas from  $0.1$  up to about  $10 \text{ km}^2$  (41.2%). Islands larger than  $10 \text{ km}^2$  (35.5%) are here considered as large islands. Figure 1 shows the geographical location of the islands included.

Not all nominal archipelagos could be analysed in terms of slope and intercept. Some of them are in fact formed by an exiguous number of islands, too few for a statistical approach. With this regard, the Tremiti Islands were excluded from the analysis which focused on the different archipelagos, whereas

all islands numbered 6–10 in Fig. 1 were pooled to compose the Sicilian island group.

### Statistical analysis

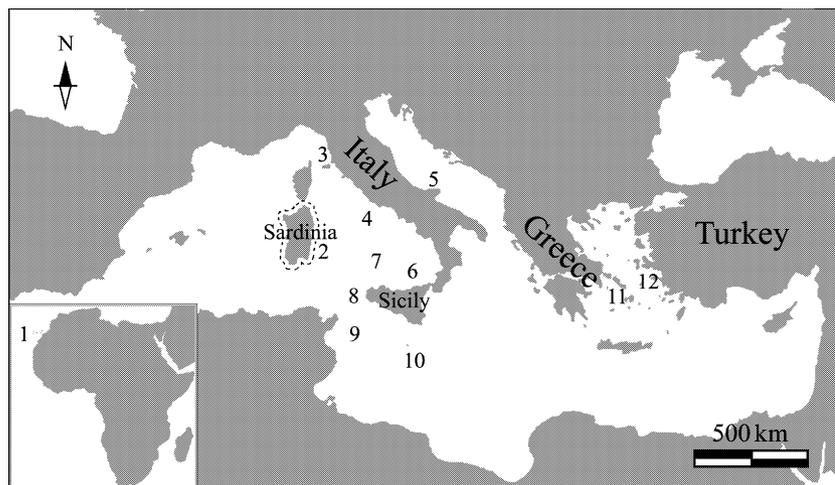
Jaccard's (1908) index and the Simple Matching index were used to investigate the similarity among islands. These indexes differ by taking, or not taking, into account 'co-absence', which, if not affected by sampling error, can be as informative as 'co-presence'. The UPGMA method was used as a clustering technique (Sneath & Sokal, 1973).

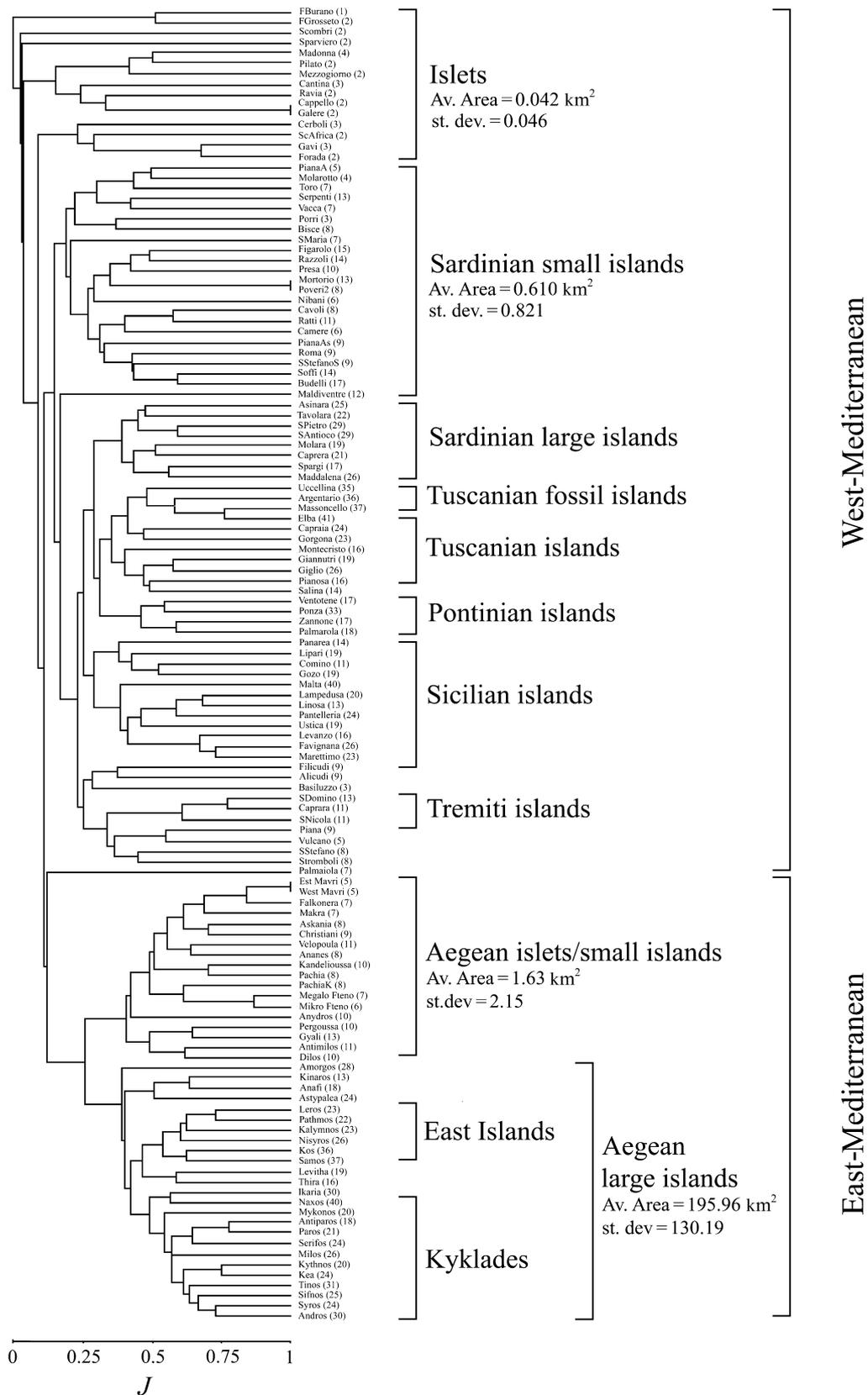
For the Tuscanian, Pontinian, Sardinian, Sicilian and Aegean islands regression coefficients have been calculated for the three regression models ( $S/A$ ,  $S/\log A$  and  $\log S/\log A$ ) that describe the relationship between the number of species and area. In an attempt to obtain a better estimate of  $z$  and  $k$  values, whose extrapolation is valid only in the range of areas represented by data (Gould, 1979), additional data concerning islets were added to the Tuscanian archipelago data set used by Sfenthourakis (1996a). We performed nonlinear regression by applying the three-parameter sigmoid equation proposed by Lomolino (2000):

$$S = \frac{a}{1 + b^{\log(c/A)}} \quad (\text{eqn } 2)$$

where  $S$  is the species number,  $A$  is area,  $a$  indicates the asymptote (maximum number of species),  $b$  is a direct measure of the slope through the inflection point, and  $c$  indicates the area at which 50% of the maximum number of species were observed. We used the coefficient of determination  $R^2$  to evaluate performance of the model. For the  $S/A$ ,  $S/\log A$  and  $\log S/\log A$  models, analysis of covariance was used to test the homogeneity of the different regression coefficients as suggested by Zar (1998). Differences among regression coefficients and intercepts have been also investigated by using the Newman–Keuls test for multiple comparisons. The test simply determines which of the slopes (or intercepts) differ. In other words, it establishes if different samples (archipelagos) come from two or more 'statistical

**Figure 1** Islands investigated. Numbers indicate the location of islands/archipelagos studied. 1, Canary Islands. 2, Sardinian islands located all around Sardinia. 3, Tuscanian islands. 4, Pontinian islands. 5, Tremiti islands. 6, Aeolian islands. 7, Ustica island. 8, Egadi islands. 9, Pelagian islands. 10, Malta. Gozo and Comino. 11, Kyklades islands. 12, Asia Minor islands.





**Figure 2** UPGMA tree based on the similarity matrix obtained by applying Jaccard's index to the binary data matrix. It is a consensus tree (50% majority rule) from the 32 slightly different trees produced by the cluster analysis. The number of species sampled in each island is in parentheses.

populations' (of islands) that differ in terms of slope (or intercept) (Zar, 1998).

To investigate the existence of a SIE, we performed breakpoint regression analyses by using both the model proposed by Lomolino & Weiser (2001) and the following discontinuous model, which combines two linear relationships into a single equation:

$$\log S = (b_0 + b_1 \log A)(\log A \leq T) + (b_2 + b_3 \log A)(\log A > T) \quad (\text{eqn 3})$$

In this equation, variables  $S$ ,  $A$  and parameter  $T$  are defined as above,  $(\log A \leq T)$  and  $(\log A > T)$  are logical variables that return 1 or 0 if true or false respectively. This model does not assume *a priori* the existence of a SIE. If a breakpoint is found, the correlation between  $\log S$  and  $\log A$  to the left of the breakpoint can still be evaluated, whereas this is not possible if equation 1 is used. The parameters were estimated by using nonlinear estimation procedures based on iteration. As in Lomolino & Weiser (2001), we incremented the breakpoint values by 0.1. Values of all parameters were chosen on the basis of the amount of variance explained (maximum  $R^2$  value).

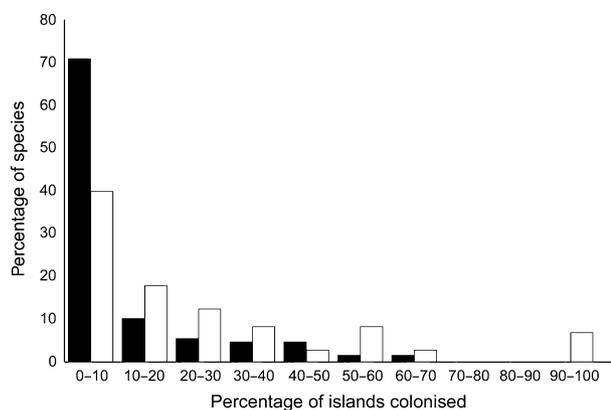
Before performing the cumulative and the sliding-windows analysis, we pooled together islands based on results from the cluster analysis. Islands below the breakpoint value, from archipelagos exhibiting a SIE, were removed from the data set. In the cumulative analysis the width of the starting window was set to 1.5 ( $\log A$ ), to include a minimum of 10 islands. The window was increased by increments of 0.1. The same width was also used in the sliding-window analysis and was also shifted by increments of 0.1.

The statistical programs NTSYS (version 2.1; Exeter Software, Setauket, NY, USA) and STATISTICA (version 5.1; StatSoft, Inc., Tulsa, OK, USA) were used. The original data set is available at the website <http://www.biogeography.org>.

## RESULTS AND DISCUSSION

### Island biogeography

The two similarity indexes provided similar results, thus, only the Jaccard's index results are presented. Figure 2 shows the UPGMA consensus tree (50% majority rule) from the 32 slightly different trees produced by the cluster analysis. This tree describes the similarity between the major Mediterranean archipelagos and it is geographically structured. Three different levels of similarity can be recognized, although clear thresholds in the similarity values cannot be easily established. According to this tree, Mediterranean islands can first be split into two distinct major faunal and geographical areas: western and eastern. In this tree, islands belonging to the Aegean archipelago form a distinct cluster, which can be divided into two groups: islets/small islands and large islands. The latter group can be further subdivided into central Aegean islands (Kykklades) and eastern islands (Asia Minor group) with different biogeographical histories. The topology of this cluster is consistent with Sfenthourakis (1996; see this publication for



**Figure 3** Evenness in the western and eastern groups of small Mediterranean islands. Bars indicate the percentage of species per percentage of islands colonized. Western and eastern island groups are indicated in black and white respectively.

a discussion of the biogeography of Aegean islands), and is not affected by the addition of the western archipelagos, which have their own identity. At a second level of differentiation, within the western Mediterranean group, islands belonging to the same archipelago were clustered together for the major part. However, they clustered at lower values of similarity compared to the similarity values at which most eastern islands are linked together. This may be due to a less even distribution of species across the western Mediterranean islands compared to the eastern archipelagos. This is highlighted in Fig. 3, which shows that more than 70% of western Mediterranean species occurred in only 10% of islands investigated.

Within the western Mediterranean cluster, a north–south geographical trend is also recognizable, with the large islands from the Tuscanian archipelago, Pontinian islands and the large islands of Sardinia all linked together. In the cluster analysis we included a few coastal hills of the Tuscanian mainland that have been permanently connected to the Italian peninsula over the last 10,000 years. We refer to these hills as 'fossil islands' (Lanza, 1984), and they clustered together with the actual islands of the present Tuscanian archipelago. It is not surprising that Elba Island (a real island) clusters within the fossil island group, since Elba Island is the largest island of the archipelago and also the most proximate to the Tuscanian coast.

The absence of a geographical structure for islands surrounding Sardinia has already been discussed by Argano & Manicasteri (1996), who considered all circum-Sardinian islands as a unique archipelago. Interestingly, the small islands of Sardinia, as well as islets of different archipelagos, did not contribute to the north–south geographical trend. Small islands from Sardinia were linked together at lower similarity values and were not directly linked to the Sardinian larger islands. Similarly, islets belonging to different archipelagos tended to cluster together at the lowest values of similarity. As shown in Fig. 2, these islets were on average much smaller and hosted a lower number of species than the Sardinian small islands. Some

geographical 'signal' was still detectable in the case of the small islands of Sardinia, which still grouped together. However, this 'signal' was completely lost in the case of islets. A similar pattern was observed by Sfenthourakis (1996b) who found that islets/very small island clusters from the Central Aegean Sea did not follow any geographical or palaeogeographical pattern, and instead were influenced by vegetation and other ecological variables. Although it is possible that the grouping of islets may have been a statistical artefact to some extent, some faunal affinity among islets/very small islands is not surprising because Oniscidea species that inhabit very small islands are relatively more common and have broader distributions than those restricted to larger islands.

On the whole, the results confirmed Oniscidea as a good biogeographical indicator and justifies the consideration of separate archipelagos in the species–area analysis.

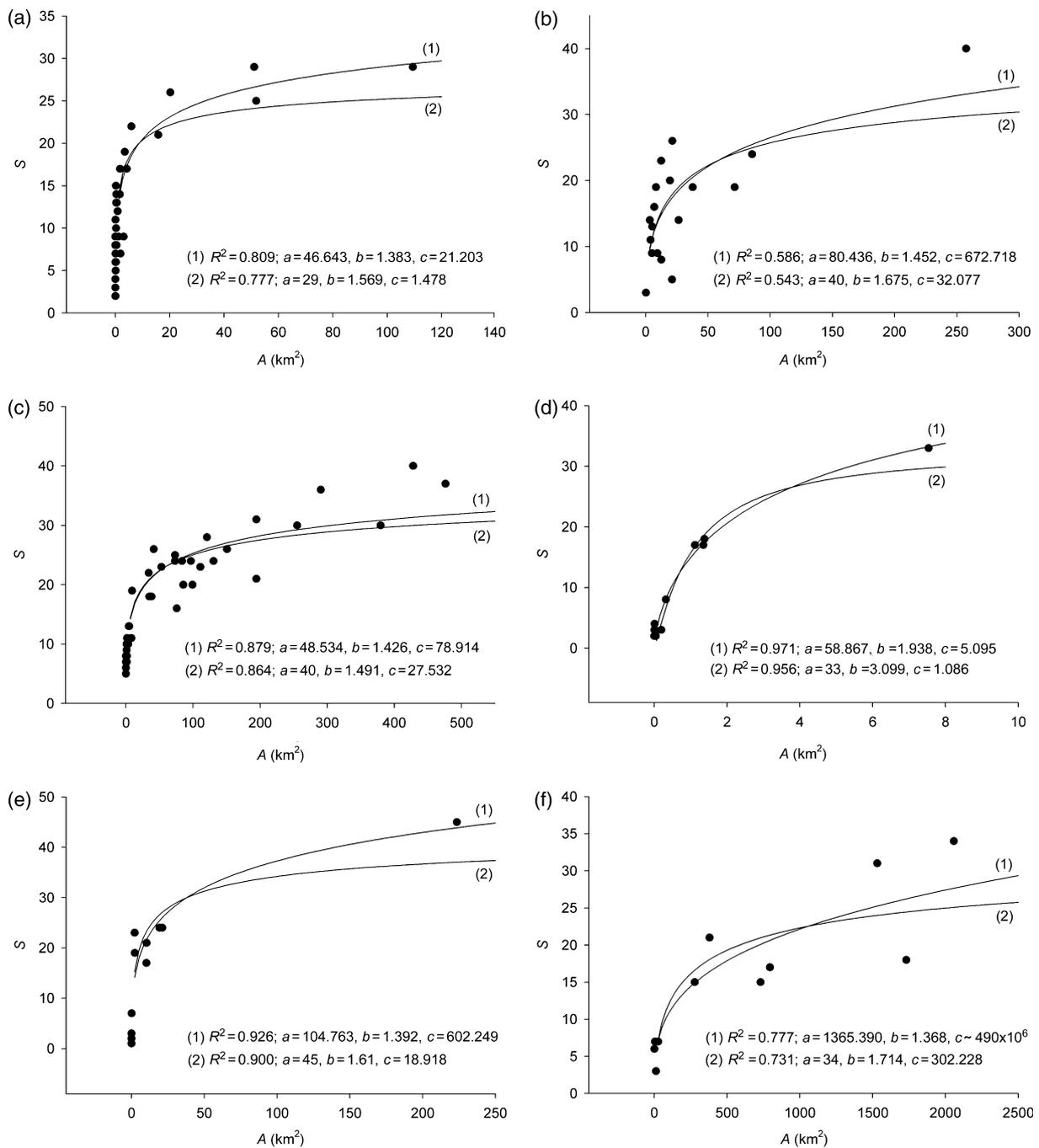
#### Island model: linear, semi-logarithmic, logarithmic and sigmoid regressions

Table 1 summarizes the results of the species–area analyses, including the breakpoint analyses. For a clearer representation, the parameters of the sigmoid regressions are presented in Fig. 4, together with their corresponding graphs. Coefficients of determination ( $R^2$ ) were generally high for all two-parameter models, but none of these models consistently

**Table 1** Regression models for species–area relationships of the Oniscidea from data derived from the literature: (1) linear; (2) semi-logarithmic; (3) logarithmic; (4) breakpoint regression (equation 1); (5) breakpoint regression (equation 3)

	$T$	% islands	$R^2$	$b_0$	$b_1$	$b_2$	$b_3$	
Sardinian (34)								
Av. area 8.12	–	–	0.502	10.253	0.244	–	–	(1)
$\sigma$ area 21.87	–	–	0.761	13.714	6.248	–	–	(2)
	–	–	0.631	1.052	0.227	–	–	(3)
	–1.47	0.088	0.670	0.690	0.245	–	–	(4)
	–1.25	0.163	0.771	–0.767	–0.845	1.075	0.204	(5)
Sicilian (18)								
Av. area 33.85	–	–	0.582	12.450	0.111	–	–	(1)
$\sigma$ area 60.46	–	–	0.538	4.568	10.351	–	–	(2)
	–	–	0.516	0.790	0.312	–	–	(3)
	–0.40	0.000	0.516	0.666	0.312	–	–	(4)
	0.60	0.111	0.580	0.764	0.720	0.849	0.265	(5)
Aegean (43)								
Av. area 82.85	–	–	0.720	12.332	0.068	–	–	(1)
$\sigma$ area 120.45	–	–	0.820	10.630	7.004	–	–	(2)
	–	–	0.920	0.977	0.199	–	–	(3)
	–0.53	0.140	0.930	0.805	0.229	–	–	(4)
	–0.30	0.140	0.938	1.048	0.210	0.926	0.229	(5)
Pontinian (13)								
Av. area 0.93	–	–	0.803	4.787	4.219	–	–	(1)
$\sigma$ area 2.06	–	–	0.742	16.439	7.311	–	–	(2)
	–	–	0.789	1.083	0.354	–	–	(3)
	–1.20	0.538	0.932	0.369	0.612	–	–	(4)
	–0.50	0.615	0.958	0.413	0.017	1.166	0.440	(5)
Tuscanian (13)								
Av. area 22.27	–	–	0.570	10.973	0.164	–	–	(1)
$\sigma$ area 60.94	–	–	0.914	14.821	9.307	–	–	(2)
	–	–	0.890	0.919	0.388	–	–	(3)
	–1.53	0.000	0.890	0.326	0.388	–	–	(4)
	–1/0.3	0.231	0.973	2.091	1.292	1.194	0.162	(5)
Canarian (11)								
Av. area 686.36	–	–	0.746	7.977	0.011	–	–	(1)
$\sigma$ area 760.54	–	–	0.677	0.173	7.227	–	–	(2)
	–	–	0.752	0.568	0.247	–	–	(3)
	1.08	0.273	0.855	0.711	0.323	–	–	(4)
	1.10	0.273	0.881	0.828	–0.206	0.423	0.303	(5)

The number of islands from each archipelago is given within brackets. Average area ( $\text{km}^2$ ) and standard deviation are reported in the first column. The breakpoint value ( $T$ , the upper SIE limit) is in the second column. The percentage of islands contributing to the upper SIE is reported in the third column. The maximum variance explained ( $R^2$ ) is indicated in the fourth column. Parameters of the regression are given in columns 5–8. Parameters  $b_0$  and  $b_2$  are intercepts, parameters  $b_1$  and  $b_3$  are slopes (see text).



**Figure 4** Sigmoid species–area relationship. (a) Sardinian islands, (b) Sicilian islands, (c) Aegean islands, (d) Pontinian islands, (e) Tuscanian islands and (f) Canary Islands. For each archipelago, the equation given by Lomolino & Weiser (2001) was calculated by using a nonlinear procedure. In case (1) parameters  $a$ ,  $b$  and  $c$  were all estimated by iteration. In case (2) parameter  $a$  was entered as a constant, with parameters  $b$  and  $c$  being estimated iteratively.  $R^2$  and estimates of parameters are shown in each graph.

provided the best fit. In particular, as already pointed out by Sfenthourakis (1996a), the logarithmic model did not always provide the best fit. A possible explanation is that the linear model may better approximate the species–area relationship when dealing with sets of data distributed in narrow size ranges. This could be because a logarithmic curve may be approximated by a linear curve when narrow intervals are

considered and also because a logarithmic transformation is less sensitive to the heteroscedasticity expected when wider ranges of area are considered (Sfenthourakis, 1996a).

The sigmoid model returned contradictory results (Fig. 4). With the exception of the Aegean archipelago, the Lomolino function provided the highest  $R^2$  values when all parameters  $a$ ,  $b$  and  $c$  were estimated (curve 1). In such cases, however,

estimates of parameters  $a$  and  $c$  returned unrealistic values for most of the archipelagos. When parameter  $a$  was entered as a constant (curve 2), parameter  $c$  became more reliable, but the amount of variance explained decreased and the sigmoid model was not the best fit. We also note that, even when it did provide the best fit, parameter  $b$  estimates were so small that the inflection point was virtually undetectable.

### Island models: slopes and intercepts in the Mediterranean archipelagos

Analysis of covariance showed that the islands from the Mediterranean archipelagos cannot be treated as belonging to the same pool ( $F = 6.642$ ,  $P_{(2),4,111} \ll 0.001$ ). Table 2 shows results of the Newman–Keuls test for multiple comparisons among slopes. Data regarding the archipelago of the Canary Islands, although available, have not been included in this test. This is because the Canary Islands are on average much larger than Mediterranean islands, and their inclusion is expected to greatly increase the variance of the data set. The Newman–Keuls test allowed us to determine which archipelagos differ in terms of slope and intercept. In terms of slope, two sets of similarities could be distinguished. The Sardinian and the Aegean archipelagos were assigned to one set. The slopes of these archipelagos were not statistically different, while their intercepts were ( $t_{(2)74} = 2.317$ ,  $P = 0.023$ ). Pontinian and Tuscanian archipelagos were assigned to the second set. Their slopes were not statistically different, whereas their intercepts were ( $t_{(2)23} = 22.495$ ,  $P \ll 0.0001$ ).

Slopes for the Tuscanian and Pontinian archipelagos have higher values than the Sardinian and Aegean archipelagos. It is instructive to note that the inclusion of six additional small islands (ranging from 0.03 to 0.1 km<sup>2</sup>) to the Tuscanian data set produced a slope estimate much higher than previously observed (Sfenthourakis, 1996a). In general, the effect of the very small islands or islets on the outcome is important because it can influence the shape and the goodness-of-fit of the species–area relationship. In general, the first part of the curve, which is important in order to detect the correct approximation, is in most cases extrapolated either because

many archipelagos lack very small islands or because the authors do not include them.

The slope for the Sicilian islands had an intermediate value and could not be assigned to any of the two sets. This is because the variance explained by the regression is very poor ( $R^2 = 0.52$ ). These results were partly expected as they possibly reflected the different degrees of isolation of the different archipelagos from their species source pools. It was reasonable to expect that geographical distance should have been related to both the species number and the rate at which species colonize islands. The last is in part reflected by the slope in the log  $S/\log A$  relationship (Rosenzweig, 1995), since intercept indicates the logarithm of the average number of species that can be found in an island of unitary area. However, for Oniscidea from the Mediterranean archipelagos studied, distance does not seem to have a great impact on species richness (Sfenthourakis, 1996a; G. Gentile & R. Argano, unpubl. data). Consistent with this view, intercepts were very similar (although their differences were statistically significant), showing values of around 1–0.9, with the only exception being the Sicilian archipelago. We do not want to over-emphasize the few statistical differences between archipelagos; however, it should be noted that the intercepts of all the continental Mediterranean archipelagos studied are higher than the intercept value of the oceanic archipelago of the Canary Islands ( $k = 0.57$ , Sfenthourakis, 1996a). It seems that geographical distance influences the rate at which the log  $S/\log A$  relationship increases. Although all of them are continental archipelagos, the Aegean islands, which exhibit the lowest regression coefficient, are on average further from the mainland than the Sicilian, and particularly the Pontinian and Tuscanian islands. The low regression coefficient observed for the Sardinian archipelago is difficult to explain. These islands are very distant from the continental mainland and this would be consistent with the low value of the slope. However, they are also extremely proximate to Sardinia, one of the largest islands of the Mediterranean Sea. Thus, a high rate of colonization could be expected from Sardinia, whereas the slope value (0.23) did not indicate this. This is most likely to be related to the number of species occurring in Sardinia (72; Argano & Manicasterri, 1996), which is much smaller than the number of species that occur in the Italian mainland ( $c. 350$ ; Argano *et al.*, 1995). It has been proposed that, for islands of equal area, slopes tend to decrease when the number of species in the original source pool (mainland) decreases (Martin, 1981). Interestingly, the  $z$ -value observed for Sardinian islands was similar to the value predicted by Schoener (1976) who, based on the observation that species differ in their dispersal and colonizing abilities and in the intensity of their interactions, provided a model to estimate  $z$  when the number of species in the mainland is known.

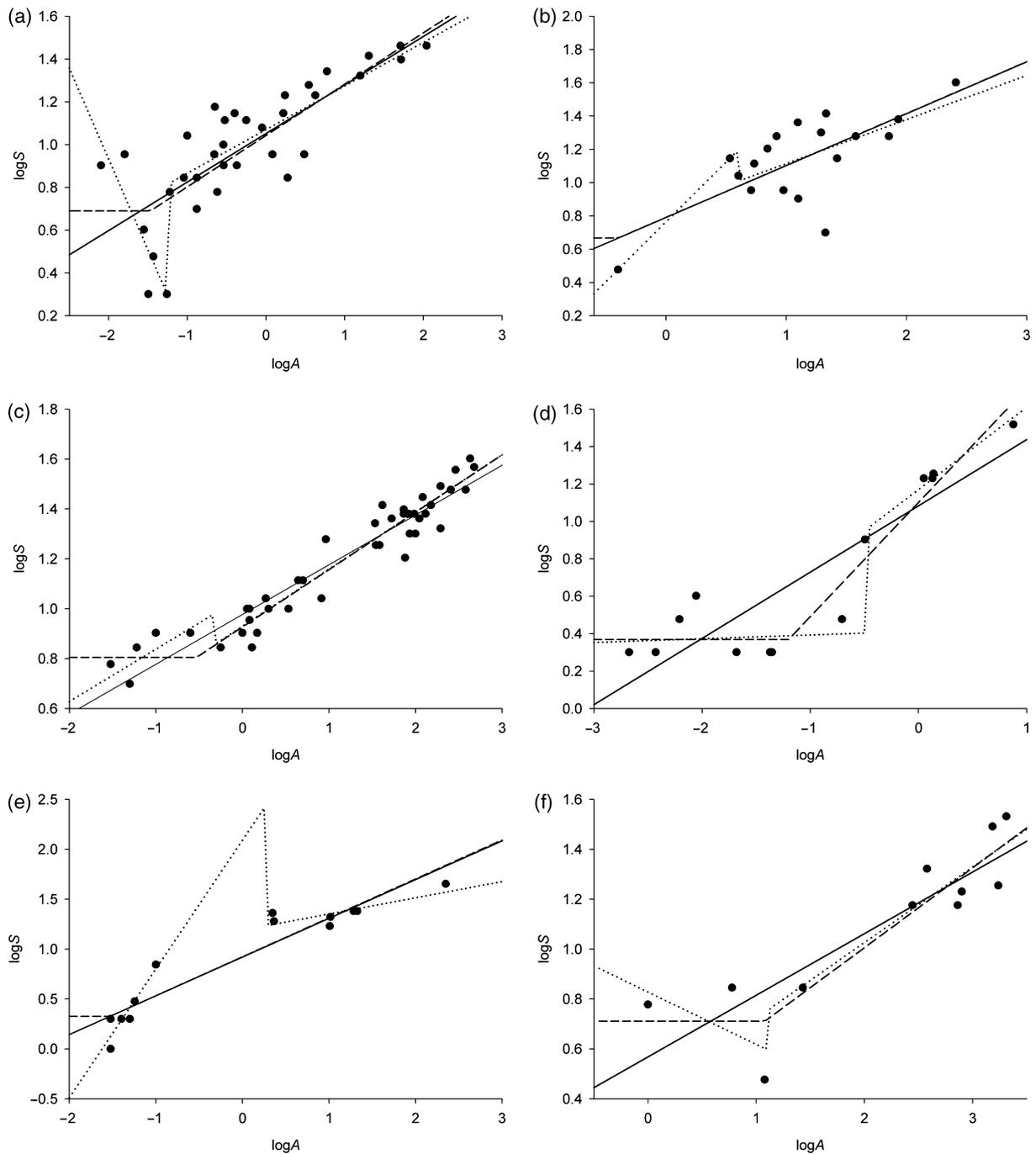
**Table 2** Newman–Keuls test for multiple comparisons among slopes of the species–area relationships for Oniscidea

	Sardinian	Aegean	Sicilian	Pontinian
Aegean tot.	1.166 (n.s.)			
Sicilian	1.771 (n.s.)	2.427 (n.s.)		
Pontinian	3.708 ( $P \ll 0.05$ )	4.834 ( $P \ll 0.01$ )	0.805 (n.s.)	
Tuscanian	5.269 ( $P \ll 0.01$ )	6.742 ( $P \ll 0.001$ )	1.526 (n.s.)	0.908 (n.s.)

The value of the observed statistic  $q$  is reported in the first row. Residual pooled DF is equal to 111. The probability that the observed  $q >$  expected  $q$  is reported in the second row (see Zar, 1998).

### Area-range effects

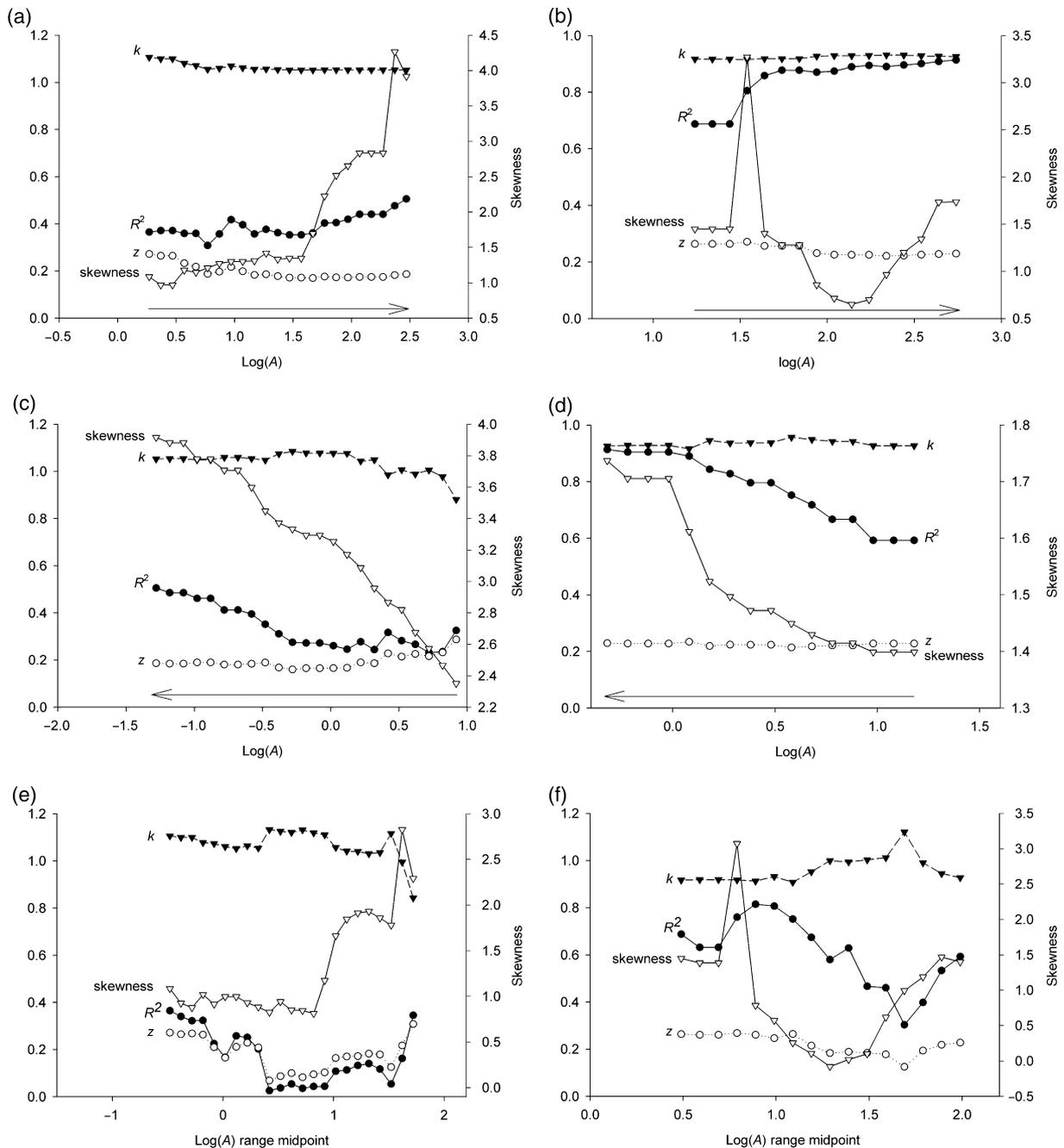
A breakpoint was found for all archipelagos (Fig. 5). Both equations 1 and 3 provided similar breakpoint values for the



**Figure 5** Species–area regressions: logarithmic regression, solid line; breakpoint regression by equation 1, dashed line; breakpoint regression by equation 3, dotted line. (a) Sardinian islands, (b) Sicilian islands, (c) Aegean islands, (d) Pontinian islands (e) Tuscanian islands and (f) Canary Islands.

Sardinian, Aegean and Canary Islands. Differences between results from the two equations were observed for the Sicilian, Pontinian and Tuscanian islands. In particular, equation 1 provided no evidence of a SIE for Sicilian and Tuscanian islands, with the breakpoint value falling outside the range of sampled islands. The breakpoint values obtained for Sicilian and Tuscanian islands by using equation 3 were in turn

dubious and should be considered with caution. For these two archipelagos, breakpoint estimates were possibly affected by large gaps occurring in the area range of sampled islands. In fact, for Sicilian islands, alternative parameter values (with slightly lower  $R^2$ ) were obtained for  $T = -0.3$  up to  $T = 0.5$ , in an area range where there are no islands. Similarly, for Tuscanian islands, the same parameter values were obtained



**Figure 6** Cumulative (a–d) and sliding-window (e, f) analyses, performed by using two subsets of data: western Mediterranean (left column), and eastern Mediterranean (right column). Determination coefficient ( $R^2$ ), slope ( $z$ ), intercept ( $k$ ) and skewness of area distribution were plotted at each step (see Introduction).

from  $T = -1$  up to  $T = 0.3$  due to the lack of islands in the corresponding interval. Thus, for these two archipelagos we prefer to consider the SIE issue as unresolved.

In general, for continental archipelagos, the breakpoint seems to occur for  $A$  smaller than  $1 \text{ km}^2$ , as Lomolino & Weiser (2001) showed for terrestrial isopods from the Aegean, by using data from Sfenthourakis (1996a). A breakpoint occurs at a higher value (*c.*  $12 \text{ km}^2$ ) for the oceanic archipelago of the Canary Islands. More data

regarding small islands and islets from this archipelago could help clarify if the higher breakpoint value observed is simply due to lack of data or if it could be an echo of the greater distance of the Canary Islands from the mainland.

Our data offer little evidence of a scale effect within the species–area relationship (Martin, 1981), although a general trend could be recognized at the inter-archipelago level (Table 1). In fact, with the evident exception only of the

Sardinian islands (which represent a special case), it seems that all the archipelagos including larger islands tend to have lower regression coefficients. If islands are included in the analysis from left to right (smaller to larger), it would be expected that  $z$  should decrease, whereas  $z$  would be expected to increase if islands are added to the analysis from right to left (larger to smaller), as in Martin (1981). Additionally, the sliding-window approach should lead to decreasing  $z$ -values when moving from left to right. The expected patterns from these analyses are poorly reflected in the results obtained (Fig. 5a–d). This approach suggests that  $R^2$  and skewness (always positive) of the area distribution may vary independently of the slope and intercept of the species–area relationships, which in turn exhibits a flattened trend for both western Mediterranean and Aegean islands. As expected, the sliding-windows analysis depicted a more accentuated trend (Fig. 6e–f), in part consistent with expectation, with  $R^2$  and skewness showing some correlation with slopes and intercepts. However, this should be taken with caution because confidence limits of values observed at each iteration partly overlap (not shown in Fig. 6 for clarity).

## CONCLUSIONS

The terrestrial isopod fauna from islands of the Mediterranean Sea can be divided into two major groups: the eastern and western Mediterranean. In general, there is a high degree of structure observed in Oniscidea assemblages from Mediterranean islands. The structure reflects evolutionary events acting at a local scale and the faunal inter-connectivity between archipelagos and the most proximate mainland. As a consequence, single archipelagos may be discriminated at different similarity values. In part, the complex biogeographical pattern may be explained by interpreting the different shapes of the species–area curves. Slopes and intercepts provide helpful hints to highlight major trends, but these data show a degree of complexity that cannot be completely explained by the models considered here. Besides the possibility that the interpretation of slopes may reflect an artefact of the regression system (Engen, 1977; Connor & McCoy, 1979; Sugihara, 1981; Keith & McGuinness, 1984), we note that several different factors may interact and eventually contribute to the values of  $z$  (MacArthur & Wilson, 1967; Karr & Roth, 1971; Willson, 1974; Gilbert, 1980). These factors make different contributions to the species–area correlation and are difficult to distinguish in most cases. In our case, some variables (latitude, number of species and species vagility) may be assumed to be acting equally on the different archipelagos, whilst others factors may not. For example, evidence was provided for a linear decrease (regressed on longitude) in the number of endemic species of reptiles from western to eastern Mediterranean islands (Mylonas & Valakos, 1990). Additionally, historical factors may play an important role in determining the colonization patterns of these archipelagos. On the whole, the effective contribution of such factors to the species–area relationship changes from case to case and cannot be easily quantified.

On the whole, area-range effects exist, although our data offered poor support for scale-dependent effects such as those discussed by Martin (1981) and Lomolino (2000). Nevertheless, most continental archipelagos considered here exhibit a SIE, with the upper limit being lower than 1 km<sup>2</sup>. Despite the occurrence of a SIE, a sigmoid model did not provide the best representation of our data. Even when the sigmoid regression returned the best fit, the inflection point was virtually undetectable. It is conceivable that in cases like this, ‘the better fit of sigmoid curves does not necessarily prove sigmoid relationships’ (Tjørve, 2003), with the better fit simply being a reflection of the flexibility of a model with a higher number of parameters.

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