

RESEARCH LETTER

The species-area relationship of terrestrial isopods (Isopoda; Oniscidea) from the Aegean archipelago (Greece): a comparative study

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Abstract. Data on species richness of terrestrial isopods (Oniscidea) from central Aegean islands (Greece), together with previously published data sets from other taxa and areas, are critically analysed under the basic premises of ecological biogeography. Habitat diversity seems to be the most important determinant of species richness for Oniscidea, although the relation to area is also significant. Comparison with other data sets demonstrates that the best fit model of the species-area relationship is case-specific and usually not unique, since the assumptions for appropriate use of any particular model ($\log S/\log A$, S/A or $S/\log A$) cannot

be satisfied by all species richness data sets, and since confidence limits around regression coefficients are usually broad for the relatively limited sizes of island groups. The values of slopes and intercepts of the species-area regression lines seem to be statistical artefacts that encompass the effects of several intervening factors, such as the data set size and range, and should be checked accordingly before any biological statements about differences between taxa or island groups can be made.

Key words. Oniscidea, island biogeography, species richness, z .

INTRODUCTION

The large number and varied sizes of the central Aegean islands (Greece) provides a good opportunity for testing certain aspects of island biogeography theory, such as the relationships between species richness, area and other factors. This much celebrated subject has appeared in only a few Aegean studies (Heller, 1976; Beutler, 1979; Mylonas, 1982) and no such study has appeared in the terrestrial isopod literature, although the oniscid fauna of several archipelagos is well known (Taiti & Ferrara, 1989; Argano & Manicasteri, 1990; Rodriguez, 1991).

There is still no general agreement on the interpretation, meaning and causality of the species-area relationship despite the extensive literature and the variety of applications and approaches to the subject (Arrhenius, 1921; Gleason, 1922; Preston, 1962; MacArthur & Wilson, 1967; Haas, 1975; Connor & McCoy, 1979; Gilbert, 1980; Lomolino, 1982; Williamson, 1988; Kelly, Wilson & Mark, 1989). The best mathematical expression of the relationship is also controversial and seems to vary between island groups

(Engen, 1977; Wright, 1988; Williamson, 1988). Finally, the interpretation of the linear equation variables z (slope) and c (intercept) is even more ambiguous (MacArthur & Wilson, 1967; Connor & McCoy, 1979; Gould, 1979; Martin, 1981; Sugihara, 1981; Wright, 1981; Abbott, 1983). Consequently, a critical approach to these subjects is necessary.

In the present paper the distributional data of Oniscidea on forty-three islands and islets of the central Aegean, Greece (Sfenthourakis, 1994) are analysed and compared with several published data sets of other taxa from the same region and of Oniscidea and other taxa of other island groups.

METHODS

Data sets

The Oniscidean distributional data have been collected during four years (1989–93) of field work on forty-two islands and islets of the central Aegean (Greece). Specimens were collected by hand in a total of 298

sampling stations, distributed in such a way that all habitat-types and geographic subdivisions of each island would have been sampled. This was accomplished by scheduling the sampling strategy after the examination of available geological, topographical and vegetational maps of islands, and by *in situ* inspection of the habitat types present on each island. Collecting was considered complete when no new species were found in more than two successive sampling stations and when all habitat types of each island had been sampled. Each sampling station covered an area of 2.5–5.0 m², depending on the local distribution of habitats. Because of the very high spatial heterogeneity of habitats on these islands, many sampling stations consisted of more than one habitat types. Effectiveness of collecting has been checked by repeated sampling on certain islands (Andros, Kea, Milos) and proved to be at the level of 90% of the total fauna, a percentage that is regarded as satisfactory for such studies. Other sampling methods (pitfall traps and litter samples) were also used during the first stages of the study, but did not give any additional species. Data given by Schmalfuss & Schawaller (1984) for the island of Thira were corrected and completed after examination of Dr M. Mylonas's collection of isopods from the Aegean and were included in the analysis, giving forty-three islands in total (Table 1).

Several ecological variables (Table 2) were recorded as present/absent at each sampling station. Habitat diversity has been calculated as the total number of these variables present on all stations of each island. For the island of Thira, habitat diversity has been estimated as the total number of the same variables that are present on the island, and has been calculated after personal observations during a recent visit to this island. This slight difference in habitat diversity estimation should not affect the analyses attempted herein because only the overall numbers of variables and species for each island are used. Between island and island to mainland shortest distances were calculated using a 1:500,000 map. Area and altitude of most islands were obtained from recent Statistical Yearbooks, while for those not recorded therein (uninhabited small islets) these data were extracted from 1:25,000 and 1:12,500 maps of the Army Geographic Agency. Limestone area was estimated from 1:50,000 geological maps.

The other data sets used in the analysis are: land snails (Mylonas, 1982) and reptiles (Mylonas & Valakos, 1990) of Kyklades, Oniscidea of the Tuscan archipelago (Taiti & Ferrara, 1989) and Canary islands

(Rodriguez, 1991) and the mammals of the Panama islands, Sunda Shelf islands and California Channel islands (Lawlor, 1986 and data sources cited therein). All these data sets, according to the above-mentioned authors, have been compiled after intensive studies and seem to be of comparable quality and reliability.

Statistical methods

The Pearson product-moment correlation coefficient has been used in estimating the correlations between number of species and island area for all groups and all cases. The standard methods of least squares linear regression and stepwise multiple regression have been used for the investigation of the relations between the dependent variable 'species number' and the independent variables 'island area', 'area of limestone', 'habitat diversity', 'altitude', 'distance from mainland' and 'distance from large islands'. Partial correlation between these variables has also been used, following Newmark (1986) who claimed that partial correlation should be used instead of stepwise multiple regression in order to avoid the bias caused by the order in which the independent variables enter into the model.

In order to compare the slopes and intercepts of linear regressions, the *F*-tests for the comparison of two and more than two slopes and intercepts, described by Zar (1984: 292–302), have been used.

RESULTS

Determinants of species richness

The species richness of Aegean Oniscidea is well correlated with area (Table 3). Since correlation does not imply causality, the influence of other parameters, such as habitat diversity, isolation and altitude has also been investigated. The results of stepwise multiple regression, using as possible predictors of species number (*S*), the area (*A*), altitude (*T*), smallest distance from nearest continental area (*D*), distance from nearest large island (*D_s*-only for islets), habitat diversity (*H*) and area of limestone (*C*-only for some large islands) for all islands, large islands, small islands (<10 km²) and large islands where limestone area was measured, are given in Table 4. Habitat diversity is the best predictor of species richness. None of the other variables entered into the model, except in the case of altitude for large islands.

In Table 5 the partial correlation coefficients among

Table 1. Environmental characteristics and isopod numbers for the Aegean Islands. Area, area of limestone, altitude, distance from nearest mainland, distance of islets from nearest large island, number of habitat variables, species number and species number previously recorded, are given for each island in this study.

| Island | Area (km ²) (<i>A</i>) | Area of limestone (km ²) (<i>C</i>) | Altitude (<i>T</i>) | Distance from nearest mainland (island) (km) <i>D</i> (<i>D_s</i>) | Number of habitats (<i>H</i>) | Species number (<i>S</i>) | Species number in literature |
|----------------|--|--|--------------------------|--|--|-----------------------------------|---------------------------------------|
| Samos | 476.2 | 400 | 1434 | 1.5 | 20 | 35 | 11 |
| Naxos | 428.1 | 240 | 999 | 120 | 19 | 38 | 20 |
| Andros | 379.7 | 102 | 994 | 11 | 19 | 30 | 14 |
| Kos | 290.3 | 88 | 843 | 4.5 | 17 | 35 | 18 |
| Ikaria | 255.3 | 10 | 1037 | 50 | 20 | 31 | 6 |
| Paros | 194.5 | 104 | 724 | 107.5 | 15 | 22 | 5 |
| Tinos | 194.2 | 23 | 725 | 51.5 | 18 | 30 | 8 |
| Milos | 150.6 | 13 | 748 | 101.5 | 15 | 26 | 5 |
| Kea | 130.6 | | 547 | 18.5 | 17 | 24 | 10 |
| Amorgos | 120.7 | 93 | 821 | 102 | 16 | 28 | 3 |
| Kalymnos | 110.9 | 93 | 676 | 16.5 | 13 | 23 | 5 |
| Kythnos | 99.3 | 15 | 255 | 38 | 16 | 20 | 7 |
| Astypalea | 96.8 | 20 | 482 | 80 | 15 | 26 | 9 |
| Mykonos | 85.5 | 5 | 372 | 85 | 13 | 20 | 5 |
| Syros | 83.6 | 10 | 432 | 58 | 16 | 24 | 15 |
| Thira | 75.8 | 6 | 564 | 167 | 13 | 18 | 17 |
| Serifos | 73.2 | 27 | 582 | 61.5 | 14 | 24 | 2 |
| Sifnos | 73.2 | 44 | 681 | 85 | 15 | 25 | 1 |
| Leros | 52.9 | 17 | 321 | 30 | 15 | 24 | 1 |
| Nisyros | 41.4 | | 698 | 17.5 | 15 | 26 | 13 |
| Anafi | 38.3 | 21 | 579 | 137.5 | 12 | 19 | 1 |
| Antiparos | 34.8 | 16 | 300 | 111.5 | 10 | 17 | 4 |
| Patmos | 34.0 | 1 | 272 | 140 | 14 | 23 | 2 |
| Levitha | 9.2 | | 130 | 65 (28.5) | 10 | 19 | 0 |
| Antimilos | 8.2 | | 671 | 97.5 (8.5) | 7 | 11 | 0 |
| Gyali | 5.0 | | 459 | 18.5 (3.5) | 10 | 13 | 0 |
| Kinaros | 4.4 | | 296 | 110 (18) | 7 | 14 | 0 |
| Dilos | 3.4 | | 112 | 49 (2) | 7 | 10 | 5 |
| Kandelioussa | 2.0 | | 103 | 39 (14) | 6 | 11 | 4 |
| Velopoula | 1.86 | | 227 | 32.5 (33.5) | 7 | 10 | 0 |
| Pachia (Kykl.) | 1.48 | | 229 | 141 (7.5) | 6 | 8 | 0 |
| Falkonera | 1.29 | | 218 | 67.5 (40.5) | 5 | 7 | 0 |
| Christiani | 1.21 | | 285 | 177 (17) | 7 | 9 | 0 |
| Pergoussa | 1.20 | | 81 | 30 (7) | 7 | 12 | 0 |
| Anydros | 1.13 | | 194 | 142.5 (16.5) | 6 | 11 | 2 |
| Pachia (East.) | 1.00 | | 137 | 29.5 (3) | 5 | 6 | 0 |
| Makra | 0.56 | | 124 | 137 (8.5) | 5 | 5 | 0 |
| Askania | 0.25 | | 171 | 190 (17.5) | 5 | 7 | 0 |
| Ananes | 0.10 | | 82 | 82.5 (19) | 5 | 8 | 0 |
| Meg.Fteno | 0.06 | | 17 | 142.5 (3) | 5 | 7 | 0 |
| West Mavri | 0.05 | | 52 | 74.5 (27.5) | 3 | 5 | 0 |
| East Mavri | 0.05 | | 40 | 75.5 (26) | 3 | 5 | 0 |
| Mik.Fteno | 0.03 | | 15 | 143 (3) | 3 | 6 | 0 |

Table 2. Ecological variables used for estimation of 'habitat diversity' (presence/absence).

| | |
|-----------------------------------|---------------------|
| Altitude | Cultivation |
| 1: 0–300 m | 17: Olives |
| 2: 300–600 m | 18: Fruit-bearing |
| 3: >600 m | 19: Herbaceous |
| Vegetation (dominant plants) | Riparian formations |
| 4: <i>Juniperus</i> spp. | 20: Arboreal |
| 5: <i>Pistacia</i> spp. | 21: Shrubs |
| 6: <i>Quercus coccifera/lilex</i> | 22: Dry banks |
| 7: Deciduous forests | Littoral zone |
| 8: Coniferous forests | 23: Sandy |
| 9: Other shrubs | 24: Rocky |
| 10: Other trees | Surface water |
| 11: <i>Sarcopoterium</i> sp. | 25: Stagnant |
| 12: <i>Cistus</i> spp. | 26: Running |
| 13: <i>Genista</i> sp. | Substrate |
| 14: Other phrygana | 27: Limestone |
| 15: Halophytes | 28: Schists |
| 16: Helophytes | 29: Volcanic |

Table 3. Pearson's product-moment correlation coefficient, r , for species number of Oniscidea (S) and central Aegean island area (A).

| Aegean islands | r | $P <$ |
|--|------|-------|
| All islands ($N = 43$) | 0.82 | 0.001 |
| Large islands ($> 10 \text{ km}^2$, $N = 23$) | 0.83 | 0.001 |
| Small islands ($< 10 \text{ km}^2$, $N = 20$) | 0.81 | 0.001 |

the above mentioned variables and species number are given. Habitat diversity is again the best predictor of species richness. The only difference with the previous analysis is that now, for small islands (islets), all other variables are also significantly correlated with S . The correlation of islets' S with altitude is negative and with distance to nearest large island positive, results that are counter-intuitive but are probably caused by the incidental isolated geographic position of relatively larger islets which are also richer in habitats.

Although the method by which habitat diversity was estimated is not robust, it should reflect a real dimension of what can strictly be termed 'habitat diversity', since it has been based on detailed observations of both the biotope structure of islands and the habitat preferences of isopod species (for the latter see Warburg, 1987 and Sfenthourakis, 1994). As a general rule, habitat diversity increases with area

and, therefore, it is not easy to make reliable claims for their relative importance (for my data set the Pearson product-moment correlation coefficient of area and habitat diversity is $r = 0.79$, $P < 0.001$, $N = 43$). The precedence of habitat diversity over area for oniscidean species richness can be inferred in a more direct way from a closer inspection of what happens on small islets. Habitat diversity on such islets depends mostly on topography, substrate, human influence, geographic position and random processes. For example, Kandeloussa with an area of 2 km^2 hosts eleven species while the nearby Pergoussa, with 1.2 km^2 , hosts twelve. The vegetation of the former island consists of drought-deciduous and seasonally dimorphic shrubs (a vegetation type called *phrygana*—Margaris, 1976), plus sparse maquis, while that of the latter is much more heterogeneous, with additional vegetational formations, such as trees and several kinds of shrubs. An even more striking example is Antimilos with an area of 8.2 km^2 and 671 m altitude but with just eleven species. Only *phrygana* are growing on this islet while on the isolated and much smaller Velopoula (area 1.86 km^2 , altitude 227 m), where there is a more variable vegetation of *phrygana* and shrubs, ten species have been found. It is clear that on small islets the vegetation structure is the major component of habitat diversity. On larger islets the presence/absence of running or stagnant water, the extension and type of cultivation,

Table 4. Stepwise multiple regressions for species number (S) of Aegean Oniscidea for the island groups discussed in the text. Independent variables were: area (A), limestone area (C), altitude (T), habitat diversity (H), distance from nearest mainland (D) and islet distance from nearest large island (D_s).

| | | |
|----------------------------|---|----------------------------------|
| All islands | $\log S = 0.15 + 1.05 \log H$ | $P < 0.001$ |
| Large islands | $\log S = 0.06 + 0.15 \log T + 0.78 \log H$ | $0.01 < P_T < 0.05, P_H < 0.001$ |
| Small islands | $\log S = 0.22 + 0.95 \log H$ | $P < 0.001$ |
| Islands (with known C): | $\log S = 0.17 + 1.04 \log H$ | $P < 0.001$ |

Table 5. Partial correlation of species number with area (A), altitude (T), habitat diversity (H), distance from nearest mainland (D) and distance from nearest large island (for islets) (D_s).

| Island group | A | T | H | $D-D_s$ |
|---------------|--------|----------|---------|---------|
| All islands | 0.20 | -0.19 | 0.61*** | -0.07 |
| Large islands | 0.04 | 0.32* | 0.57*** | -0.14 |
| Small islands | 0.38** | -0.51*** | 0.64*** | 0.47*** |

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

as well as other dimensions of habitat diversity are also important. Many of these have been included in the above mentioned measure of diversity.

The species-area relation

Relationships between species number (S) and area (A) have usually been expressed by one or more of the following three models: (a) the power function model, approximated by the double log transformation ($\log S / \log A$), (b) the exponential model ($S / \log A$) and (c) the linear model (S/A). The results of their application on the data of the various island groups are given in Table 6. The central Aegean islands have been separated into the Kyklades and eastern (near Asia Minor) islands, in order to check for isolation effects. Correlation coefficients are highly significant in all models, except for S/A and $S / \log A$ of Panama mammals. Best-fit lines were determined from the percentage of variance explained (r). As can be seen, each model fits best to some of the data sets while in most cases more than one model fits equally well by taking into account the confidence intervals for the regression coefficient r . These are relatively broad as a result of the small data set sizes that are used in biogeographical studies. This problem is inherent to species-area data because of the trivial fact that most island groups are composed of few islands. Ignoring this effect we can generally see that the $\log S$ - $\log A$ model fits better to all central Aegean (Fig. 1), Kyklades and Canary islands Oniscidea, to Panama mammals and to Kyklades

reptiles. The S/A model fits better to large and small Aegean island and Tuscan archipelago Oniscidea, and to Sunda Shelf and California Channel island mammals. Finally, the $S / \log A$ model fits better to eastern Aegean island Oniscidea and Kyklades land snails. The total number of species and the total number of islands used in each case do not seem to play any role in the determination of the best-fit models.

The best fit lines of Aegean Oniscidea could be regarded as echoing the problem of heteroscedasticity that is intrinsic to species-area data sets. Heteroscedasticity owing to increasing variance of species numbers with increasing area is greater in data sets with a wider range of area. In these cases logarithmic transformation more efficiently linearizes the species-area curve. Therefore the $\log S / \log A$ model expectedly fits better to the complete data set and to the Kyklades (where most islets occur), while the S/A model is best for the subgroups of Aegean islands (small, large) with narrower area range.

Comparison of slopes and intercepts

The slope (z) of the $\log S / \log A$ regression line ranges as follows: (i) 0.16 to 0.33 for mammals, (ii) 0.16 to 0.23 for Oniscidea in the subdivisions of the present study area, (iii) 0.16 to 0.24 for Oniscidea in general, (iv) 0.27 for the land snails of the Kyklades, and (v) 0.38 for the reptiles of the Kyklades (Table 6). Before differences in z between taxa or areas can be attributed to biological factors it is important to check for the

Table 6. Results of least squares linear regressions for the several island groups and regression models discussed in the text. The best fit model in each case is given in bold. Numbers in parentheses under names of island groups are the total number of species and total number of islands respectively, c.i.=confidence intervals for r at $\alpha=0.05$.

| Islands | Model | z | c | r | c.i. | r^2 | $P<$ |
|------------------------|-----------------------|---------------|--------------|-------------|------------------|--------------|--------------|
| Aegean Oniscidea | <i>S/A</i> | 0.06 | 12.59 | 0.82 | 0.69–0.90 | 68.1 | 0.001 |
| All islands | log/log | 0.20 | 0.97 | 0.95 | 0.91–0.97 | 90.1 | 0.001 |
| (71, 43) | <i>S/log A</i> | 6.99 | 10.71 | 0.92 | 0.86–0.96 | 84.1 | 0.001 |
| Large islands | <i>S/A</i> | 0.03 | 20.16 | 0.83 | 0.74–0.92 | 69.7 | 0.001 |
| (>10 km ²) | log/log | 0.20 | 0.98 | 0.77 | 0.52–0.89 | 59.7 | 0.001 |
| (67, 23) | <i>S/log A</i> | 12.58 | −0.20 | 0.79 | 0.57–0.91 | 62.5 | 0.001 |
| Small islands | <i>S/A</i> | 1.09 | 6.89 | 0.81 | 0.66–0.92 | 65.6 | 0.001 |
| (<10 km ²) | log/log | 0.16 | 0.95 | 0.78 | 0.52–0.91 | 61.0 | 0.001 |
| (37, 20) | <i>S/log A</i> | 3.41 | 9.63 | 0.75 | 0.46–0.89 | 56.4 | 0.001 |
| Kyklades | <i>S/A</i> | 0.07 | 11.33 | 0.84 | 0.70–0.92 | 70.7 | 0.001 |
| (59, 31) | log/log | 0.19 | 0.97 | 0.95 | 0.90–0.98 | 90.3 | 0.001 |
| | <i>S/log A</i> | 6.30 | 10.86 | 0.91 | 0.82–0.96 | 83.1 | 0.001 |
| Eastern | <i>S/A</i> | 0.05 | 16.2 | 0.81 | 0.45–0.94 | 65.7 | 0.005 |
| (53, 12) | log/log | 0.23 | 0.95 | 0.95 | 0.84–0.98 | 90.4 | 0.001 |
| | <i>S/log A</i> | 9.74 | 7.85 | 0.97 | 0.90–0.99 | 94.2 | 0.001 |
| Tuscan | <i>S/A</i> | 0.11 | 20.09 | 0.97 | 0.82–1.00 | 93.8 | 0.001 |
| Oniscidea | log/log | 0.16 | 1.19 | 0.81 | 0.15–0.97 | 65.6 | 0.005 |
| (65, 7) | <i>S/log A</i> | 11.40 | 12.17 | 0.83 | 0.20–0.97 | 68.9 | 0.005 |
| Canary | <i>S/A</i> | 0.01 | 8.05 | 0.86 | 0.54–0.96 | 73.9 | 0.005 |
| Oniscidea | log/log | 0.24 | 0.57 | 0.86 | 0.54–0.96 | 74.8 | 0.001 |
| (66, 11) | <i>S/log A</i> | 7.11 | 0.32 | 0.82 | 0.44–0.95 | 67.7 | 0.005 |
| Kyklades | <i>S/A</i> | 0.06 | 18.92 | 0.75 | 0.46–0.89 | 55.7 | 0.001 |
| land snails | log/log | 0.27 | 0.88 | 0.81 | 0.58–0.92 | 66.0 | 0.001 |
| (88, 24) | <i>S/log A</i> | 14.09 | 0.32 | 0.82 | 0.60–0.92 | 66.6 | 0.001 |
| Kyklades | <i>S/A</i> | 0.028 | 5.22 | 0.66 | 0.18–0.89 | 43.4 | 0.01 |
| reptiles | log/log | 0.38 | 0.13 | 0.72 | 0.28–0.91 | 51.8 | 0.005 |
| (15, 13) | <i>S/log A</i> | 2.67 | −4.05 | 0.70 | 0.24–0.90 | 49.3 | 0.005 |
| Panama | <i>S/A</i> | 0.005 | 2.99 | 0.26 | — | 6.62 | 0.5 |
| mammals | log/log | 0.33 | −0.08 | 0.57 | 0.03–0.85 | 32.43 | 0.05 |
| (?, 13) | <i>S/log A</i> | 2.26 | 0.041 | 0.51 | — | 26.55 | 0.1 |
| Sunda Shelf | <i>S/A</i> | 0.0002 | 15.09 | 0.94 | 0.87–0.97 | 89.02 | 0.001 |
| mammals | log/log | 0.25 | 0.54 | 0.92 | 0.83–0.96 | 83.91 | 0.001 |
| (?, 27) | <i>S/log A</i> | 19.89 | −28.2 | 0.89 | 0.77–0.95 | 79.31 | 0.001 |
| California Channel | <i>S/A</i> | 0.012 | 1.06 | 0.89 | 0.65–0.97 | 80.06 | 0.001 |
| mammals | log/log | 0.17 | 0.08 | 0.89 | 0.65–0.97 | 78.81 | 0.001 |
| (?, 12) | <i>S/log A</i> | 0.78 | 1.34 | 0.79 | 0.41–0.94 | 63.08 | 0.01 |

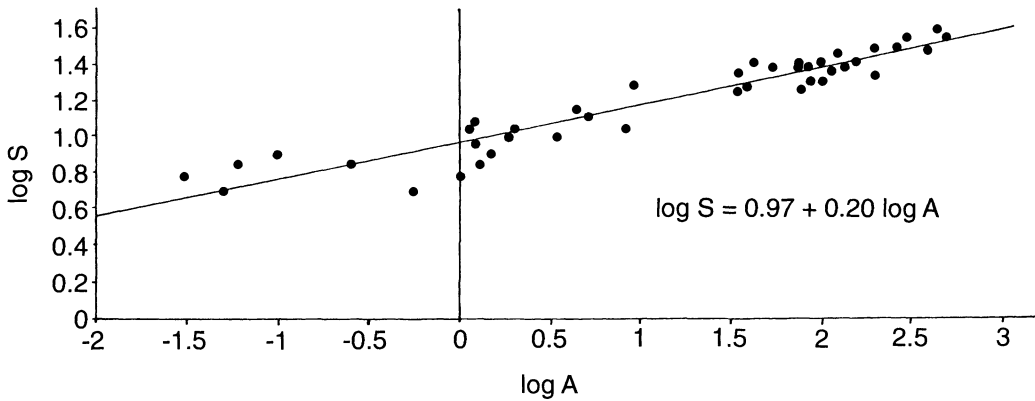


Fig. 1. The least squares regression of species number (S) on island area (A) (log/log model) for central Aegean Oniscidea (all islands).

Table 7. Comparisons of regression slopes (log S /log A model) between island groups and taxa discussed in the text. H_0 is that slopes do not differ.

| | | |
|-------------------|--------------------------------------|--------------------|
| Oniscidea | | |
| (TUS-AEG-CAN) | $F = 1.42 < F_{0.05(1)2,55} = 3.18$ | H_0 not rejected |
| (AEG-TUS) | $t = 0.82 < t_{0.05(2)46} = 2.01$ | H_0 not rejected |
| (AEG-CAN) | $t = 1.29 < t_{0.05(2)50} = 2.01$ | H_0 not rejected |
| (TUS-CAN) | $t = 0.87 < t_{0.05(2)14} = 2.14$ | H_0 not rejected |
| Aegean | | |
| (ONI-REP-MOL) | $F = 2.47 < F_{0.05(1)2,74} = 3.11$ | H_0 not rejected |
| (ONI-REP) | $t = 1.58 < t_{0.05(2)52} = 2.01$ | H_0 not rejected |
| (ONI-MOL) | $t = 1.83 < t_{0.05(2)62} = 1.99$ | H_0 not rejected |
| (MOL-REP) | $t = 0.81 < t_{0.05(2)33} = 2.03$ | H_0 not rejected |
| Mammals | | |
| (PAN-CHAL-SUN) | $F = 2.12 < F_{0.05(1)2,46} = 3.2$ | H_0 not rejected |
| All island groups | $F = 1.67 < F_{0.05(1)7,134} = 2.09$ | H_0 not rejected |

Abbreviations: ONI, Oniscidea; REP, Reptiles; MOL, Mollusca; AEG, Aegean; TUS, Tuscan; CAN, Canary; PAN, Panama; CHA, Channel; SUN, Sunda Shelf.

Table 8. Comparisons of regression intercepts (log S /log A model) among the Oniscidean species-area relations. H_0 is that intercepts are not different. Abbreviations as in Table 7.

| | | |
|---------|------------------------------------|----------------|
| AEG-TUS | $t = 9.41 > t_{0.05(2)46} = 2.02$ | H_0 rejected |
| AEG-CAN | $t = 8.25 > t_{0.05(2)51} = 2.008$ | H_0 rejected |
| CAN-TUS | $t = 3.34 > t_{0.05(2)15} = 2.13$ | H_0 rejected |

possibility that they are only statistical artefacts. All comparisons resulted in statistically indistinguishable slopes (Table 7). On the other hand, the comparison of intercepts revealed significant differences among Oniscidean regressions (Table 8).

Such statistical tests do not often appear in the numerous discussions of the species-area relation (but see Nilsson, Bengtsson & As, 1988) although it is not reasonable to invoke biological explanations for differences among variables when these differences are

non-existent. The remarks of Gould (1979) on the correct use of z and c (compare intercepts only when slopes are the same and vice versa) have to be evaluated for such cases of superficially differing variables. In the case of Oniscidea, assuming identical slopes, the Canary islands have the lowest intercept ($\log c = 0.57$), the Tuscan archipelago the highest ($\log c = 1.19$) and the Aegean islands are intermediate ($\log c = 0.97$), reflecting patterns of species richness per unit area (larger in the Tuscan archipelago, lower in the Canary islands). This result has a reasonable biological explanation, since the Canary islands are isolated, oceanic and with a lower total number of species, while the Tuscan archipelago is close to the rich mainland species-pool of Italy. The central Aegean islands are intermediate although they are also continental, lying in-between the mainlands of Greece and Turkey. Their lower species richness, compared to the Tuscan archipelago, may be attributed to the drier climate, more extensive human influence and to the more episodic geological past (longer isolation of Kyklades).

CONCLUSIONS

Species richness of central Aegean Oniscidea is most strongly related to the measure of habitat diversity employed in this study, but correlation with island area is also very high. Other factors, such as isolation and altitude did not have any significant influence on Oniscidean species richness. These results are of local importance only, as can be inferred by examining the species richness of small islets. In other places, with different topography, geological history, climate, habitat types, etc., other processes may lead to different responses of species richness. Such differences are revealed in comparisons between data sets. Determination of species richness is complex and there cannot be a single monothetic model (such as the 'area *per se*' or the 'habitat diversity') explaining it.

Results with more general applicability come from the comparative analysis of the species-area relationship models and the comparisons of 'different' slopes. Two points deserve emphasis.

First, each of the linear models, supported as best descriptors of the species-area relation by several authors, provides the best fit to some of the data sets. At the same time, all models are statistically acceptable in most cases. The best fit model depends on the distribution of points on a species-area scattergram which cannot be directly translated to biological

processes since it is a product of the distributions of both the data-set-specific island sizes and the species richness range. Also, the statistical assumptions for appropriate use of each model (see for example Zar, 1984) are not universally true for biogeographical data. Since patterns of abundance do not determine species-area relations (Wright, 1988), the use of any particular model (usually the $\log S / \log A$) should be regarded as a result of convenience in order to facilitate comparisons between different studies.

Second, the statistical non-difference of several superficially varying slopes is caused by data-set size effects on the regression line. Part of this problem, namely the effect of area-range on z , has been stressed by Martin (1981). However, the total number of islands and the range of species richness also affect the values of the regression parameters. For example, the presence of fewer mammal or reptile species per unit area than molluscs or isopods is more or less universal, but there is also differential representation of the same animal group among different areas (e.g. Oniscidea on the Canary islands and the Tuscan archipelago), whereas the number and size range of islands are never identical nor even similar between most island groups. These data set variations produce a wide range of slopes and intercepts that do not have any explanatory value by themselves nor as absolute values.

It is obvious that we should be more careful with the use and evaluation of simplified models in explaining patterns of biological diversity. An elementary precaution in studies of island biogeography should be the control of data set size-and-range effects when comparing species-area curves.

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