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A comparison of relict versus dynamic models for tenebrionid beetles (Coleoptera : Tenebrionidae) of Aegean Islands (Greece)

Simone Fattorini

Dipartimento di Biologia Animale e dell'Uomo (Zoologia), Università di Roma "La Sapienza"
Viale dell'Università 32, I-00185 Rome, Italy

ABSTRACT. This paper analyses the species-area relationship in the Aegean tenebrionids in order to discriminate between relict and dynamic models. Using different statistical approaches, the following eco-geographic variables were tested as predictors of the tenebrionid richness on 32 Aegean Islands : latitude, longitude, area, maximum elevation, distance to the mainland, and distance to the nearest island. Area was identified as an important predictor, while neither distance to the mainland nor distance to the nearest island was identified as of any statistical importance in affecting tenebrionid richness. Thus, as proposed for other very sedentary animals inhabiting this archipelago such as land snails, a relict model is postulated. As most tenebrionids have extremely limited ability to actively disperse over the sea, ancestral species have probably colonised the Aegean Islands by means of land-bridges during Pleistocene falls in the sea level.

KEY WORDS : Island Biogeography, relict models, Greece, Coleoptera, Tenebrionidae.

INTRODUCTION

The large number and varied sizes of the Aegean Islands make this archipelago excellent material to study the species-area relationship in insular biotas. Tenebrionids (Coleoptera, Tenebrionidae) are primarily saprophagous beetles, which occur in a great variety of habitats, being ideal objects for studies of ecological biogeography in different environments, such as forests, steppes, deserts and urban habitats (see FATTORINI, 2000 and references therein). Their highly diversified ecology can be an important property, especially for the study of insular faunas, which are generally characterised by low diversity. In fact, tenebrionids can be a rare case of a group that also appears rich in species in these circumstances, allowing for a study based on a large set of species.

According to vicariance biogeographers, present distribution patterns are more dependent on the subdivision of ancestral biotas in response to changing geography than on dispersal abilities. However, an understanding of a group's vagility is a prerequisite for any biogeographic study because species with higher dispersal ability are obviously less affected by vicariance events (e. g. NOONAN, 1988). Most Tenebrionidae are characterised by aptery. As vagility of apterous beetles is greatly reduced by their inability to fly, tenebrionids are a group of great interest in historical biogeography (FATTORINI, 2000). In particular, as many tenebrionids are strictly resident organisms with extremely limited ability to actively disperse over the sea, these beetles may be of particular interest in insular biotas strongly affected by historical events.

The tenebrionid fauna of the Aegean Islands is mostly composed of apterous species. However, these apterous species also occur in the adjacent mainland areas (i. e. Greece and Anatolia) or, if endemic, belong to apterous genera (cf. FATTORINI et al., 1999). Therefore, aptery in Aegean tenebrionids evolved before island colonisation, and it is not a consequence of living on islands. Although aptery greatly reduces the beetles' ability to actively disperse, other dispersal mechanisms, such as rafting and water transport, cannot be a priori dismissed as factors assisting island colonisation by apterous tenebrionids. For example, phylogeographic data on flightless Canarian tenebrionids strongly support models of sequential invasions affected by inter-island distances (JUAN et al., 1997, 1998 ; VARGAS et al., 1999), thus suggesting that recent

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Corresponding author : S. Fattorini, e-mail : tenebrio@hotmail.com

dispersal played an important role in determining their present distribution patterns.

The geological history of the Aegean Islands has been evoked as an important factor in their biogeography (SFENTHOURAKIS, 1996). Before the Serravallian (12-14 Ma), the Aegean area was substantially occupied by a continental environment without marine ingressions. In the Serravallian, the Anatolian block started to move westwards, originating the southward extension of the Aegean plate. During the lower Tortonian (11 Ma), massive marine ingressions occurred in the northern and southern Aegean, and in the late Pliocene (4 Ma), as a result of subduction of the African oceanic lithosphere, the southern Aegean was submitted to tectonic uplift. Around 3-2 Ma, the Cyclades land mass was submerged, thus originating the Cyclades islands (WELTER-SCHULTES & WILLIAMS, 1999). However, as a consequence of glaciations, the coastline of the Mediterranean Basin has significantly changed since the Pleistocene. Therefore, the biogeographic characteristics of the Aegean Islands during the Pleistocene (notably their size and distance to the mainland) were very different from the present. In particular, many islands were joined to each other and to the adjacent mainland (cf. DERMITZAKIS, 1990; OLIVIER, 1993; SFENTHOURAKIS, 1996; WELTER-SCHULTES & WILLIAMS, 1999).

This historical scenario can obviously be responsible for differences in distributional patterns. As a rule, one can suppose that, in the same area, sedentary taxa are strongly affected by historical processes, whereas present ecological factors may be more important in conditioning the distribution of taxa with higher dispersal abilities. Therefore, in a given area, different animal groups should conform to different biogeographic models.

Relict models postulate that present distribution patterns of insular faunas are more dependent on historical factors (such as the palaeogeographic connections between islands and mainland areas followed by vicariance events) than present conditions (such as island distance to the mainland). According to the relict models, a positive species-area relationship results from area-dependent extinction or relaxation (cf. CROWELL, 1986). By contrast, dynamic models suppose that distribution patterns are more influenced by present conditions (especially island distance to the mainland and inter-island distances) than by historical factors.

The dynamic equilibrium model of island biogeography proposed by MACARTHUR & WILSON (1967) postulates that the effect of island area on species number is due to equilibrium between immigration and extinction. According to this model, immigration rates are enhanced by an island's proximity to a source of species (e.g. a mainland area), and large islands have lower extinction rates than do smaller islands, because their larger populations are less vulnerable to stochastic events. Two main predictions follow: (1) the number of species will increase with area; (2) species richness will decrease with distance. Note that these two predictions can also be made under different assumptions. According to CONNOR & MCCOY (1979), large islands may have more species simply because they 'sample' more individuals, and hence more species, from the total pool of immigrants. CONNOR & MCCOY (1979) do not deal with isolation effects on the passive sampling. However, one can reasonably admit that far distant islands should 'sample', and hence retain, fewer species than islands closer to the mainland. In both the equilibrium and the sampling models, an area *per se* effect is supposed, and species number on islands is regarded as a consequence of present colonisation (dispersal from the mainland). Therefore, they involve only dynamic processes.

By contrast, according to WILLIAMS (1964), large areas have more species because they have more habitats than do small areas (habitat diversity model). Also in this case, distance would have a negative effect on species richness; comparing islands with the same habitat diversity, far islands are more difficult to be reached by mainland populations and they would consequentially harbour fewer species. However, the habitat diversity model is also compatible with relict models, because one can suppose that different islands were reached by immigrants in past times, and that they retained more or less species according to their habitat diversity. In this scenario, if habitat diversity is positively correlated with area, large islands are expected to have retained more species, while, as the geography of the study area changed, no relationships are expected between species richness and distance. By contrast, as distance negatively affects present colonisation processes, both the equilibrium and the sampling models should be rejected, if no negative relationships can be observed between species richness and distance. In such circumstances, a relict model should be accepted and a habitat model can be evoked to explain a positive species-area relationship. Note that a habitat model could be also evoked in non-relict faunas, when species richness is positively correlated with habitat diversity (but not with area) and negatively with distance.

In this paper, I analyse the species-area relationship in the Aegean tenebrionids in order to discriminate between relict and dynamic models.

MATERIAL AND METHODS

Study area

The Aegean Islands are located in the East Mediterranean, between the Greek and Turkish coasts. They are mainly aligned in a NW-SE direction and embrace various large islands (including Kriti, Euboea and some north-eastern islands), as well as some fringing archipelagos (i. e. Northern Sporades, Southern Sporades and the Cyclades). The climate of the Aegean Islands is typically Mediterranean. Phrygana is the dominant vegetation type throughout the islands, while forest and maquis habitats occur only in scattered patches on some of the largest islands. Forests are characteristically represented by oak (*Quercus coccifera*) forests, which, most probably, were the climax vegetation type of the Aegean area (Polunin & Walters, 1985), and pine (*Pinus halepensis*, *P. brutia* and *P. nigra*) forests. Habitat changes determined by human activities, especially deforestation, are an important key feature of the ecology of many of the islands. For example, the Cyclades have been inhabited for at least 4500 years and most arable land was cleared and hillsides terraced over two millennia ago. However, while forests were seriously affected by human activities, maquis habitats are relatively well preserved and the phrygana has been greatly extended as a result of deforestation (cf. Runemark, 1971; Simberloff, 1986; Olivier, 1993), thus presumably favouring xerogeophilous tenebrionids.

On some islands, human activities may have caused extinction of a few tenebrionid species associated with forest habitats. However, xylophilous species represent a minor component of the tenebrionid fauna considered here (about 15 out of 133 species). Therefore, as for other animal groups such as terrestrial isopods and land snails (Sfenthourakis, 1996; Welter-Schultes & Williams, 1999), the low number of species that could be presently absent on some islands as a result of extinction, is not expected to have any substantial influence on the overall species numbers.

Data sources

A total of 32 Aegean Islands were included in this study (Fig. 1, Table 1). Due to intensive research from the beginning of the past century to the present, all these islands are faunistically well known. These islands are

TABLE 1

Tenebrionid richness and untransformed eco-geographic variables for the studied islands. *S* = Tenebrionid richness, *La* = latitude (°N), *Lo* = longitude (°E), *A* = area (Km^2); *E* = elevation (m); *Di* = distance to the nearest island (Km), *Dm* = distance to the nearest mainland (Km).

Island	***S***	***La***	***Lo***	***A***	***E***	***Di***	***Dm***
Amorgos	7	36.5	25.59	121.1	821	12.8	104
Anafi	12	36.21	25.5	38.4	582	20.8	140
Andros	12	37.45	24.42	380	994	2	57
Castellorizon	8	36.08	29.34	7.3	271	120.8	2
Chios	10	38.22	26	842	1297	20	11
Euboea	42	38.34	23.5	3658	1745	11.2	0.3
Folegandros	7	36.37	24.54	32.1	415	14.4	132
Ios	9	36.42	25.24	107.8	713	6.6	147
Karpathos	15	35.4	27.1	301	1215	1	93
Kea	6	37.34	24.22	130.6	560	8.8	20.5
Kimolos	3	36.48	24.34	35.7	358	1.2	102
Kithnos	4	37.25	24.28	99.3	306	8.8	36
Kos	26	36.5	27.1	290.3	843	4	3.5
Kriti	70	35.29	24.42	8260	2456	36.8	99
Lemnos	10	39.54	25.21	460	459	24	59
Lesvos	17	39.1	26.2	1630	968	51.2	10.5
Mikonos	10	37.29	25.25	85.5	372	2.4	114
Milos	19	36.41	24.15	150.6	751	1.2	100
Naxos	36	37.02	25.35	428	1001	5.8	130
Pano Koufonissi	12	36.56	25.59	3.8	114	0.6	147
Paros	8	37.08	25.12	194.5	705	1.6	116
Rhodos	41	36.1	28	1400	1215	8.2	21
Samos	14	37.48	26.44	476.2	1434	5.6	2.8
Santorin	26	36.24	25.29	31	586	20.8	173
Serifos	8	37.11	24.31	73.2	585	12	64
Sifnos	9	36.59	24.4	73.2	678	12	87
Sikinos	8	36.39	25.06	41	533	6.6	144
Siros	23	37.26	24.54	83.6	422	16.8	75
Skiros	11	38.53	24.32	209	792	52	75
Skopelos	7	39.1	23.4	96	680	3.2	21
Thasos	13	40.41	24.47	379	1203	57.6	6
Tinos	13	37.38	25.1	194.3	730	8	80

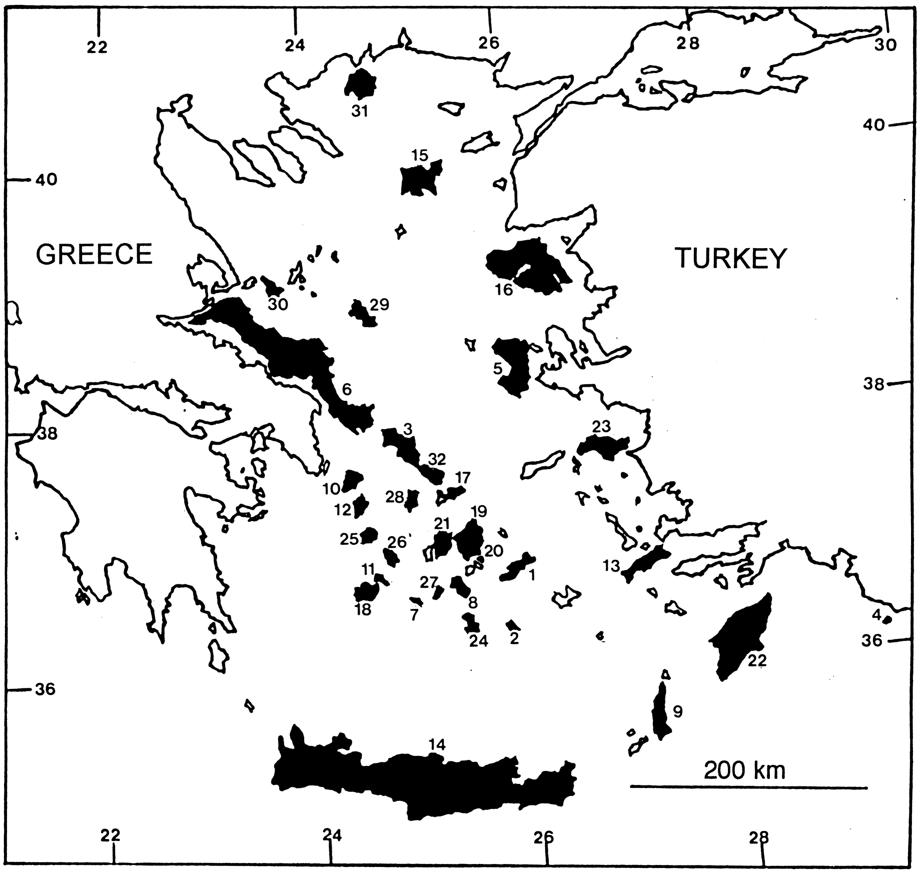

Fig. 1. – Map of the study area. Studied islands are in black. 1 Amorgos, 2 Anafi, 3 Andros, 4 Castellorizon, 5 Chios, 6 Euboea, 7 Folegandros, 8 Ios, 9 Karpathos, 10 Kea, 11 Kimolos, 12 Kithnos, 13 Kos, 14 Kriti, 15 Lemnos, 16 Lesvos, 17 Mikonos, 18 Milos, 19 Naxos, 20 Pano Koufonissi, 21 Paros, 22 Rhodos, 23 Samos, 24 Santorin, 25 Serifos, 26 Sifnos, 27 Sikinos, 28 Siros, 29 Skiros, 30 Skopelos, 31 Thasos, 32 Tinos.

also well distributed throughout the whole Aegean area and are representative of different ecological conditions. On the Aegean Islands, several species are represented by different subspecies endemic to individual islands or groups of islands. No island except Kriti has more than one subspecies of a given species. In contrast, Kriti, the largest Aegean island, harbours different subspecies of some species. It is difficult, at present, to state the actual taxonomic status of these Cretan populations. These subspecies occupy different areas on Kriti, and, probably, also different habitats. Therefore, they should be subject to the same biogeographic determinants as species in the species-area relationships. Generally speaking, large islands, having larger areas and / or more habitats, may harbour more subspecies than small islands, where reduced areas do not allow allopatric differentiation or habitat segregation. For these reasons, I have counted these populations as different taxa. As a whole, 166 species and subspecies (133 species) were ascertained to occur on the study islands as native. Note that if only the species level is used for the tenebrionid richness of Kriti, we found a value of 58 species, which is rather lower than that of 70 obtained by counting both species and subspecies. For comparison, I have performed all analyses using two sets of data: one with the value of 70 species and subspecies, the other with that of 58 species. However, both sets gave comparable results. Therefore, only results obtained by using both species and subspecies are extensively discussed. For simplicity, the term 'species' will be used in reference to tenebrionid richness, including subspecies for Kriti.

Figures reported in Table 1 are almost entirely based on data cited by Fattorini et al. (1999). Other literature records, not quoted by Fattorini et al. (1999), but included in this study, were taken from Liebegott (1982), Whitehead (1997), Grimm & Schawaller (2000), Scupola & Lo Cascio (2001) and Leo & Fattorini (in press). New records for Karpathos (an undetermined specimen of *Stenosis*, in bad condition, coll. S. Fattorini) and Rhodes (*Menephylus cylindricus* (Herbst, 1784) and *Leichenum* sp., P. Leo, personal communication) were also included. The systematic treatment of the genus *Colpotus* was updated following Grimm & Schawaller (2000). As to the genus *Pimelia*, I considered *P. subglobosa* Pallas 1781 as monotypic and synonymous with *P. sericella* Solier 1836 (Fattorini & Leo, unpublished data).

I have omitted some species, cited by various authors from the study islands, because they are synanthropic (and thus possibly introduced), transient, exotic or of uncertain distribution. A detailed account of the criteria used to reject data can be found in FATTORINI et al. (1999). I have also omitted the whole subfamily Alleculinae, and, within the subfamily Lagrinae, the tribe Lagriini, because they are taxonomically and faunistically very poorly known. Although Lagriini and Alleculinae, both winged taxa, were omitted, other winged species, with high dispersal power, are included in the data set (e. g. *Anemia sardoa* (Géné, 1839), *Cossyphus tauricus* Steven, 1829, *Diaperis boleti* (Linné, 1758), *Hypophloeus* spp., *Nalassus plebejus* (Küster, 1850), *Pentaphyllus chrysomeloides* (Rossi, 1792), *Trachyscelis aphodioides* Latreille, 1809, etc.).

As a whole, even if some islands are better known than others (Kriti and some of the Cyclades are the best studied) and new records can be expected, the very slight differences between the numbers of taxa recorded here and those quoted several years ago by DAJOZ (1987) suggest that future increases in species numbers will not be substantial.

Data analysis

To study the relation between species and area, three different mathematical models have been used by various authors (cf. CONNOR & MCCOY, 1979; WHITTAKER, 1998): the linear function model ($S = C + zA$, where S is the number of species, A is the area and C and z are constants), the exponential function model ($S = \mathrm{Log}C + z\mathrm{Log}A$), and the power function model ($S = CA^z$ approximated by the double Log-transformation: $\mathrm{Log}S = \mathrm{Log}C + z\mathrm{Log}A$). There is no a priori biological reason to insist either or both variables be Log-transformed, and the best-fit model for a particular species-area curve can usually only be determined empirically (cf. CONNOR & MCCOY, 1979). These three mathematical models have different properties, and they have been widely used to study the species-area relationship in a great number of archipelagos (e. g. CONNOR & MCCOY, 1979; WHITTAKER, 1998), including the Aegean Islands (cf. SFENTHOURAKIS, 1996a). Thus, for the purposes of comparison, I investigated the species-area relationship by using all these functions. The standard method of least squares linear regression has been used for all functions.

The power function model actually poses some statistical and biological problems outlined by WRIGHT (1981) and WILLIAMS (1995, 1996). WRIGHT (1981) pointed out that if the error term is multiplicative the logarithmic transformation is correct, while if the error term is additive the logarithmic transformation is incorrect. According to WRIGHT (1981), as the error in S is probably independent of A, the logarithmic transformation is incorrect and a non linear least-squares fit should be used. However, I think that the error in S can be dependent on A. It is reasonable to suppose that faunas of small islands, having fewer species, can be completely known. By contrast, large islands, harbouring a great number of species, are more difficult to be completely known. Thus, we can presume that our degree of faunistical knowledge (i. e. our estimate of S) is associated with area, and the logarithmic transformation may be appropriate. In addition, in nonlinear regression, the parameter estimates are too heavily influenced by large values, causing shortcomings in the use of this technique (WELTER-SCHULTES & WILLIAMS, 1999). To avoid some biological problems of the power function, WILLIAMS (1995, 1996) proposed the cumulative extreme-value function (EVF). However, when WELTER-SCHULTES & WILLIAMS (1999) compared results obtained by using the EVF and the power function, the two functions gave substantially the same results; the same authors also found that fitting the power function model using non linear regression was of questionable utility. Therefore, as in other recent studies (e. g. MILLIEN-PARRA & JAEGER, 1999; RICKLEFS & LOVETTE, 1999; KOTZE et al., 2000), in this paper the power function in its linear form was applied instead of the EVF or a non linear function.

The influence of area has also been investigated with other procedures, together with the following other geographic parameters: latitude, longitude, elevation, distance to the mainland, and distance to the nearest island.

As in other studies (e. g. NEWMARK, 1986), maximum elevation was intended here to represent a rough estimate of potential habitat diversity. Many variables, claimed to reflect habitat diversity, do not measure this factor at all (NILSSON et al., 1988); in addition, some measures that can be appropriate for some organisms may be not appropriate for organisms with other ecological preferences. This fact may represent an important, and usually overlooked, bias when a group that includes a large set of species with different ecological preferences is studied. As to the tenebrionids, this group occurs on the Aegean Islands with species that have a great variety of ecological preferences, including both xylophilous species (which occur in rotten wood and associated cambium and subcortical spaces, feeding on wood, fungi, or even on other beetles) and geophilous species (which occur on the ground, even in littoral regions, where they can be encountered beneath dune plants or in sea weed, carrion, or other organic debris). In this case, rather than direct measures of habitat diversity, a synthetic, indirect measure, may be preferable. As elevation is correlated with temperature, precipitation, humidity, wind speed, evaporation and insolation, it may be an indirect, 'universal' measure of habitat diversity.

The Shapiro-Wilks W test was used to test if species richness and eco-geographic variables followed normal distributions. Species richness, longitude, elevation, area and distance to the nearest island showed substantial deviation from normality. Therefore, these variables were $\log_{10}$-transformed to improve normality. By contrast, both latitude and distance to mainland showed normal distributions; therefore both these variables were left untransformed.

The Pearson product-moment correlation coefficient was used in estimating the correlations among the eco-geographic variables and between them and species richness. A sequential Bonferroni correction (Rice, 1989) was used to adjust the significance level to the number of comparisons (*k*) using the same data set.

A partial correlation analysis was conducted between species richness and the eco-geographic variables to identify the 'isolated effects' of each of these variables (cf. Newmark, 1986).

For the purposes of comparison, a forward stepwise multiple regression between species richness and eco-geographic variables was also performed. Using this type of multiple regression, the independent variables are individually added or deleted from the model at each step of the regression until the 'best' regression model is obtained. Both area (positively) and latitude (negatively) contributed significantly to the model. However, the negative correlation between species richness and latitude could be actually due to the location at low latitudes of Kriti and Rhodes, two large islands that harbour a great number of species. As multiple regression results were consistent with partial correlations, they will not be treated further in this paper.

Also, when independent variables are highly correlated (such as area and elevation in this study), a multiple regression analysis can be affected by multicollinearity problems. To remove the multicollinearity and reduce the number of predictors, the predictors can be replaced by their principal component scores. This procedure may be also appropriate when different parameters might not, taken one by one, have important effects, but they could be statistically significant when taken all together or by pairs. Thus, a Factorial Analysis using a Principal Component Analysis (PCA) was performed with a VARIMAX normalised rotation on the eco-geographic variables. The three principal components (factors) with an eigenvalue higher than one were retained and the loadings examined to find their relationships with the original variables: F1 was mainly area and elevation, F2 was mainly longitude, and F3 was mainly latitude. As the principal components were uncorrelated (orthogonal) they were used as replacements for the original eco-geographic variables into a forward stepwise regression analysis. Only F1 contributed significantly to the model, thus confirming results obtained from previous analyses, without adding extra information. Therefore, the results obtained from this analysis will not be treated further.

In all tests, a minimum probability level of $p < 0.05$ was accepted (all tests were two-tailed). Statistical analyses were performed using STATISTICA software (version 4.5, 1993).

RESULTS

Species-area relationships

Species richness was significantly correlated with area of the Aegean Islands for all the three models (Fig. 2). As to the percentage of variance explained, the linear function model was the best fit, accounting for about 70% of the total variance. The exponential function model accounted for about 40% of the variance, and the power function model for about 35%. However, it should be noted that the R^2 goodness-of-fit statistic is not strictly appropriate for estimating the relationship between observed and predicted values of *S*. On the contrary, the appropriateness of a model should be judged by the lack of systematic error (Sugihara, 1981). Therefore, the standard error of the estimate (S_{yx}), and not the correlation coefficients should be used (Lobo & Martín-Piera, 1999), to check the appropriateness of the three models. Using the standard error of estimate, the power function

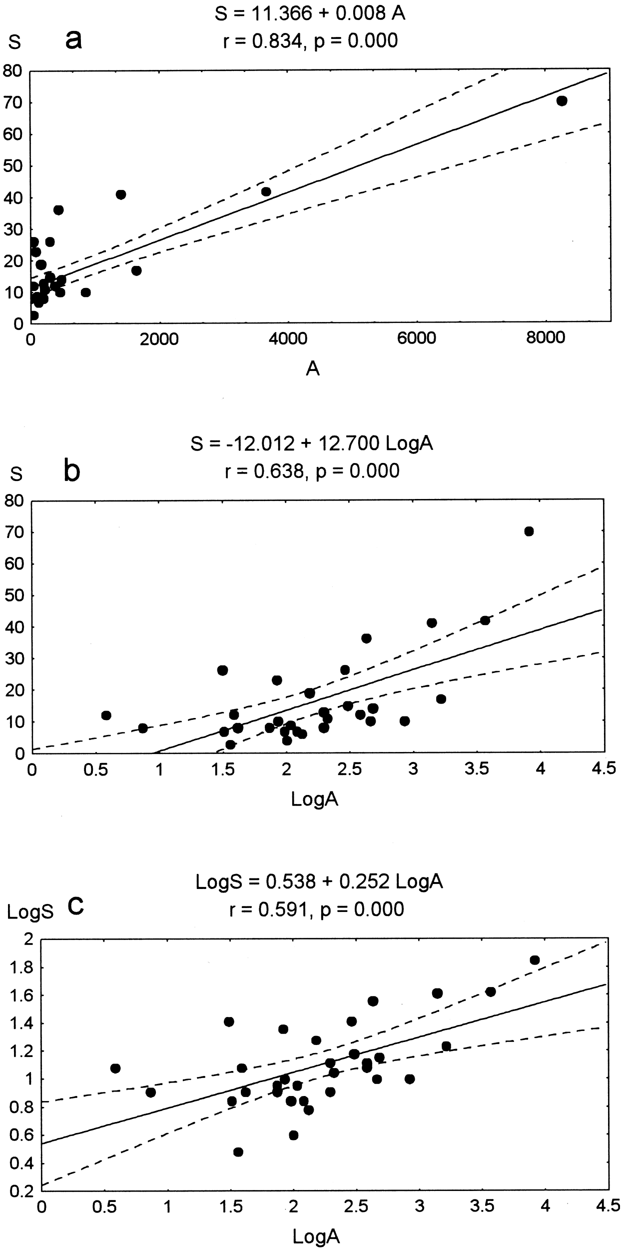

Fig. 2. – Species-area relation for tenebrionids of the Aegean Islands: a) linear function, b) exponential function, c) power function. Dotted lines correspond to 95% confidence limits.

appeared to be the best fit (S_{yx} = 0.246; actually it is the standard error of Log$S$; the standard error to be considered is that of S_{yx} = 1.761). Both the linear (S_{yx} = 7.860) and the exponential (S_{yx} = 10.966) models gave higher S_{yx}.

The species and subspecies number of Kriti (70 species and subspecies) is slightly inferior to that predicted by the linear function model (73.29), but much higher than would be expected from its area alone using the other models (33.48 with the power function, and 37.73 with the exponential model). Note that if the value of 58 species is used, the following predicted values are found: 63.66 with the linear function ($S = 11.762 + 0.006A$, r = 0.776, p = 0.000, S_{yx} = 8.085); 32.12 with the power function (Log$S$ = 0.556 + 0.243Log$A$, r = 0.582, p = 0.000, S_{yx} = 1.749); and 35.10 with the exponential function (S = -9.447 + 11.373Log$A$, r = 0.635, p = 0.000, S_{yx} = 9.909).

Correlation among variables

The following correlations were found among the eco-geographic variables: latitude with distance to the mainland (r = -0.513, p = 0.003), area with elevation (r = 0.874, p = 0.000), and area with distance to the mainland (r = -0.443, p = 0.011). However, the correlation of area with distance to the mainland did not resist the Bonferroni correction (k = 15).

The tenebrionid richness was positively correlated with both area (r = 0.591, p = 0.000) and elevation (r = 0.573, p = 0.000), also after the Bonferroni correction (k = 6). No correlation was found between species richness and other variables.

Partial correlation analysis

Partial correlation analysis showed that only area was significantly correlated with tenebrionid richness after holding latitude, longitude, elevation, distance to the mainland and distance to the nearest island constant (Table 2). These results suggest that only area *per se* is significantly correlated with tenebrionid richness when the effects of latitude, longitude, elevation, distance to the nearest island and distance to the mainland are removed, but that all these variables are not significantly correlated with species richness when the effect of area is removed.

TABLE 2

Partial correlations between tenebrionid richness (dependent variable) and eco-geographic variables (independent variables). The partial coefficient indicates correlation between the respective variable and the dependent variable, after controlling for all other independent variables.

Eco-geographic variables	r_{partial}	**p-level t(26)**
Latitude	-0.158	0.430
Longitude	0.231	0.245
Area	0.410	0.033
Elevation	0.023	0.909
Distance to the nearest island	0.135	0.501
Distance to the nearest mainland	0.256	0.196

DISCUSSION

A positive, statistically significant correlation between area and tenebrionid richness was found using linear, exponential and power functions. The power function model represented the best fit model. The z-value of 0.252 is very close to that (0.263) predicted by theory (e. g. SUGIHARA, 1981). However, after decades of intensive study of the species-area relationship (e. g. MACARTHUR & WILSON, 1967; MAY, 1975; CONNOR & MCCOY, 1979; GOULD, 1979; MARTIN, 1981; SUGIHARA 1981; WRIGHT, 1981; CROWELL, 1986; NEWMARK, 1986; NILSSON et al., 1988; SFENTHOURAKIS 1996a; LOBO & MARTÍN-PIERA, 1999; WELTER-SCHULTES & WILLIAMS, 1999), the question whether or not the values of z have any importance for ecological communities remains unresolved. Also, if the 0.20 to 0.40 range is considered as the null hypothesised range of slopes, only slope values deviating from this range should have biological significance (CONNOR & MCCOY, 1979). As the value observed in this study falls in the 0.2-0.4 range, the subject will not be treated further in this paper.

As to the C value, GOULD (1979) suggested that, when slopes are constant in families of related curves, C values could be compared as a size-independent invariant within a system. For the Aegean area, the C values of the power function model for land snails ($S = 9.48A^{0.18}$, WELTER-SCHULTES & WILLIAMS, 1999) and isopods ($S = 9.33A^{0.20}$, SFENTHOURAKIS, 1996a) can be compared with that observed for the tenebrionid beetles ($S = 3.45A^{0.25}$). It appears that, regardless of island size, the biota contains about three species of land snails and isopods (2.75 land snail species, 2.70 isopod species) for each tenebrionid species. This fact may suggest that (1): tenebrionid species require greater habitat extensions than do land snails or isopods (possibly because of the large size of some species such as those belonging to the genera *Tentyria*, *Akis*, *Pimelia* and *Blaps*, which can exceed 15-20 mm in length) and / or (2) tenebrionids are less able colonists (or, in other words, that they occur on islands mainly as relict species, as expected for very sedentary animals).

Distances to the nearest island and to the mainland were not identified as of any statistical importance in affecting species number. Lack of correlation between species number and island distance to the nearest island suggests that no ‘stepping stone’ processes are involved in determining tenebrionid species richness. According to dynamic models, species richness should be negatively related to the distance to the mainland. In this study, the distance to the mainland does not affect tenebrionid species richness. Therefore, as proposed for other very sedentary animals such as the land snails (Welter-Schultes & Williams, 1999), a relict model can be postulated for the present tenebrionid faunas on the Aegean Islands.

As tenebrionids have extremely limited ability to actively disperse over the sea, they have probably colonised the Aegean Islands by means of land-bridges during Pleistocene falls in the sea level.

During the Pleistocene regressions, most of the Cyclades were connected to each other, and their distances to the Balkan coasts were generally reduced or disappeared, while the Southern Sporades were connected to the Anatolian mainland (cf. Strid, 1970; Beutler, 1979; Dermitzakis & Sondaar, 1981; Dermitzakis, 1990; Sfenthourakis, 1996; Welter-Schultes & Williams, 1999; and references therein). Tenebrionid species with very low dispersal abilities may have reached a continuous distribution between the mainland and present islands areas during the Pleistocene falls in the sea level. When the sea level was restored, islands became isolated and the ancestral populations occupying both mainland and island areas were subject to vicariance events, being divided into insular and mainland populations.

Palaeogeographic factors are probably involved also in the levels of endemism of the Aegean tenebrionids. During the Pleistocene lowering of the sea level, most of the remote islands were mutually connected, forming various Pleistocene groups of islands. As suggested by Fattorini et al. (2000), these various island groupings were presumably located at different distances to the mainland, accounting for a positive correlation between proportion of sub-endemic taxa (i. e. taxa occurring on islands of the same group but not on islands of other groups) and distance to the mainland; only few islands were completely isolated, evolving strictly endemic taxa.

However, present dispersal can not be completely rejected a priori, at least for some species. Generally speaking, rafting, wind and water transport, frequently evoked as important factors that can assist island colonisation, may play an important role in determining long-distance chance dispersal especially for beetles associated with sandy shores (cf. Howden, 1977). Based on data summarised by Krestenitis (available at http ://archimedes.civil.auth.gr/krestenitis/en/aegean.html) the complex circulation of the Aegean Sea can be sketched as follows. The prevailing winds in the Aegean Sea are summer northerly dry winds that cause a flow toward the south along the Greek coast and give rise to a two-gyre system, respectively in the west and in the east. In the summer, the North Atlantic waters enter the south Aegean Sea from the passages east and west of Kriti, forming a two-gyre system. There is also an eastward flow along the north coast of Kriti giving rise to a cyclonic circulation in the Cretan Sea. In the winter, an overall surface circulation exists with a northerly current along the Anatolian coast and a southerly current along the Greek coast. Although this type of circulation seems to be favourable to inter-island exchanges and island colonisation by mainland populations, the lack of correlation between species richness and island distance to the mainland or inter-island distance suggests that sea circulation cannot be evoked as a major factor in determining present distribution patterns. The present hydrodynamics of the Aegean Sea could be actually involved in the distribution of some strictly psammophilic species, which could be subject to over-water dispersal on 'rafts'. However, they are represented by few species, occurring on few islands, and are not expected to have any substantial influence on the general patterns here outlined.

For the Aegean tenebrionids as a whole, island area was the eco-geographic parameter accounting for most variability in species number. This agrees with the findings of Welter-Schultes & Williams (1999) concerning land snails and with those of Sfenthourakis (1996a) concerning land isopods. By contrast, the importance of elevation in determining tenebrionid richness is equivocal. A positive correlation between tenebrionid richness and elevation was observed by using the Pearson product-moment correlation, but not confirmed by partial correlations.

Interestingly, based on stepwise multiple regression and partial correlation analyses, Sfenthourakis (1996a), who used both elevation and particular measures of habitat diversity (obtained as a sum of the presence of different types of environmental variables), found a correlation between isopod species richness and habitat diversity, but not between species richness and elevation. However, using the Pearson product-moment correlation coefficient, a positive correlation between species number and Log-transformed elevation (r = 0.799, p = 0.000) can be detected also for the Sfenthourakis data.

The enhanced number of tenebrionid species associated with higher island elevations may indicate that an increased number of potential habitats may increase species richness. Actually, higher islands may contain a greater range of potential habitats, and so are richer in habitat types than low islands of the same area. On the other hand, partial correlations suggest an effect of area *per se*, while elevation appears uncorrelated with tenebrionid richness. As pointed out by Nilsson et al. (1988), to clearly differentiate between the effects of area *per se* and habitat diversity on species richness, it is necessary to study a system where these variables are uncorrelated. Unfortunately, in the Aegean Islands studied here, area and elevation were strictly correlated. Thus, it is not possible to give any definitive conclusion on this topic.

Using the power function and the exponential function, the tenebrionid richness of Kriti appears to be much higher than would be expected from its area alone. An observed value greater than predicted values has been also recognised for land snails by Welter-Schultes & Williamms (1996), and probably reflects the palaeogeographic history of Kriti. During the lower Tortonian (11

Ma), massive marine ingressions in the northern and southern Aegean caused the separation of six or more islands in the region of present-day Kriti, which were joined only 3-2 Ma. This long isolation time allowed the species' populations on the palaeoislands to diverge sufficiently to become different species or subspecies (cf. WELTER-SCHULTES & WILLIAMMS, 1996). The high species and subspecies number for Kriti (22 of which are endemic, see FATTORINI et al., 2000), thus reinforces that the Aegean tenebrionids are relictual, not equilibrial.

CONCLUSIONS

As suggested by CROWELL (1986), the essential feature of equilibrium is continued immigration and extinction. Whereas enhanced distances affect species number in dynamic models by reducing immigration rates, distance is not an important determinant of species richness for relict faunas undergoing relaxation. As observed for land snails (WELTER-SCHULTES & WILLIAMS, 1999), the tenebrionid fauna of the Aegean Islands is not affected by distance effects. Therefore, this study rejects dynamic models as a principal or important cause of tenebrionid species richness on the Aegean Islands. Also, in accordance with the findings of WELTER-SCHULTES & WILLIAMS (1999) on Aegean land snails, area and possibly island elevation are identified as the most important factors affecting species number. As these two variables are highly correlated, it is not possible at present to discriminate between habitat diversity and area *per se* effects.

Although area and / or habitat availability together with historical effects have been the major factors in determining the species-area relationships, many other factors such as vegetation type and extent, anthropic pressures, or the presence of sandy beaches, may have concurred to determine the present-day island tenebrionid richness on each island. However, for most of the Aegean tenebrionids the effects of these factors are as yet unknown. For example, the maximum elevation of the island is an obviously important factor for some orophilic species such as *Asida fairmairei* Boieldieu, 1865 or *Pedinus subdepressus* Brullé, 1832. The occurrence of wooded areas (presently strongly reduced by man) is an important factor for those species either directly associated with trees, such as *Helops coeruleus* (Linné, 1758), *H. rossii* Germar, 1817 and *Nalassus plebejus* (Küster, 1850), or indirectly associated with this habitat, such as *Hypophloeus fraxini* Kugel, 1794 and *H. pini* Panzer, 1799 (both likely predators on scolitid beetles). Presence of well-preserved sandy shores and dunes is crucial for the life of psammophilic species such as *Ammobius rufus* Lucas, 1849, *Phaleria acuminata* Küster, 1852, *P. bimaculata* (Linné, 1767), *Trachyscelis aphodioides* Latreille, 1809, *Xanthomus graecus* Dajoz, 1984, and *X. ovulum* (Seidlitz, 1898).

However, new insights and more investigation are needed to ascertain the importance of present-day ecological factors in determining the tenebrionid distribution patterns in the Aegean. Further knowledge of the species' ecology may also clarify if area acts indirectly on species number through presence and absence of particular habitat types.

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