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AEGEAN ISLANDS
SPECIES-AREA RELATIONSHIP
ISLAND BIOGEOGRAPHY
EXTINCTION

ABSTRACT. – The aim of this paper was to investigate geographic patterns of tenebrionid (Coleoptera Tenebrionidae) endemicity on the Aegean Islands (Greece). These beetles are known to have an impressive non adaptive radiation on the Aegean Islands. Levels of endemism appeared poorly influenced by present geography or island shape, while past land configurations appeared to have a major role, as expected for flightless beetles, more affected by past vicariance events than by present dispersal. Extinction events observed in the study area exceeded largely those which a model based on the species-area relationship could predict even for a disproportionate amount of area (habitat) loss, possibly as a consequence of the particular relict condition of the Aegean fauna.

INTRODUCTION

The study of the levels of endemism has been largely applied for making decisions about conservation of species and areas (Myers & De Grave 2000, Cook & MacDonald 2001, Sfenthourakis & Legakis 2001). Several authors considered as a measure of endemism the extent of occurrence of each species within a geographic area, the most restricted ones receiving higher scores (e. g. Lumaret & Lobo 1996, Kier & Barthlott 2001, Laffan & Crisp 2003). However, the relationships between levels of endemism and area's characteristics have been poorly explored (Vilenkin & Chikatunov 1998, 2000). Also, endemicity is not linked to the size of the area, but corresponds to the exclusive occurrence of a species in that area (Myers & De Grave 2000). As in any biodiversity study involving area definition (see Peterson & Watson 1998), the concept of endemism implies, to be applicable, to establish the geographic limits of the areas for which a species is considered endemic or not. As islands are unambiguously defined, island endemics are the species restricted to an island alone. From an archipelago perspective, species occurring in more than one island, but not outside the archipelago, can be considered subendemic to the islands and endemic to the archipelago. Thus, islands represent a rare case where the concept of endemicity can be applied unambiguously. The importance of the study of endemism levels on islands is enhanced by the conservation concern of island endemics, because island populations are more prone to extinction than mainland ones, with island endemics having higher extinction rates than nonendemic ones (Frankham 1998). Thus islands represent an excellent subject to study how levels of endemism are affected by geographic parameters and to explore the possible implications of such relationships from a conservation standpoint. The aim of this paper is to investigate geographic patterns of tenebrionid (Coleoptera Tenebrionidae) endemicity on the Aegean Islands (Greece), with emphasis on their conservation interest. I chose the tenebrionids of the Aegean Islands because of three main reasons. First, tenebrionids are an important group in the structure and functioning of Mediterranean insular biotas (Cartagena & Galante 2002). Second, the tenebrionid fauna of most Aegean Islands has been taxonomically and faunistically fully revised recently and distributional data can be considered complete and accurate enough (Fattorini *et al.* 1999, Fattorini 2000, 2002a, b). Third, the tenebrionid fauna of the Aegean Islands is of high biogeographic interest because of its great non adaptive radiation and of high conservation interest because of its acknowledged importance in determining endemicity hotspots (Sfethourakis & Legakis 2001).

Specifically, I studied here: (1) the influence of island characteristics (geography and shape) on levels of endemicity; (2) the incidence of species extinction on individual islands; (3) the relationships between percentage of extinct species and biogeographic categories; (4) the extent of species loss occurred in recent time in comparison with the number of extinct species expected by virtual reduction in habitat/area size.

MATERIAL AND METHODS

Study area and data source: A total of 32 Aegean Islands were included in this study (Table I). These islands are well studied, well distributed throughout the whole Aegean area and

Table I. – Composition of the tenebrionid beetle fauna and geographic variables from each of the 32 evaluated Aegean Islands. A = area (Km²), La = latitude (°N), Lo = Longitude (°E), E = elevation (m asl), Di = distance to the nearest island (Km), Dm = distance to the nearest mainland (Km), P = perimeter (Km), S = Tenebrionid richness (number of species and subspecies), END = number of endemic taxa, SUB = number of subendemic taxa.

Island	A	La	Lo	E	Di	Dm	P	S	END	SUB
Amorgos	121.1	36.50	25.59	821	12.8	104	112	7	0	2
Anafi	38.4	36.21	25.50	582	20.8	140	32	12	0	3
Andros	380	37.45	24.42	994	2	57	177	13	1	2
Castellorizon	7.3	36.08	29.34	271	120.8	2	19	8	1	0
Chios	842	38.22	26.00	1297	20	11	213	10	0	0
Euboea	3658	38.34	23.50	1745	11.2	0.3	678	42	1	0
Folegandros	32.1	36.37	24.54	415	14.4	132	40	7	0	2
Ios	107.8	36.42	25.24	713	6.6	147	81	9	0	1
Karpathos	301	35.40	27.10	1215	1	93	160	15	0	3
Kea	130.6	37.34	24.22	560	8.8	20.5	81	6	1	0
Kimolos	35.7	36.48	24.34	358	1.2	102	38	3	0	1
Kithnos	99.3	37.25	24.28	306	8.8	36	98	4	0	0
Kos	290.3	36.50	27.10	843	4	3.5	112	26	0	4
Kriti	8260	35.29	24.42	2456	36.8	99	1046	71	20	7
Lemnos	460	39.54	25.21	459	24	59	259	10	0	0
Lesvos	1630	39.10	26.20	968	51.2	10.5	370	17	0	1
Mikonos	85.5	37.29	25.25	372	2.4	114	81	10	0	4
Milos	150.6	36.41	24.15	751	1.2	100	126	19	1	3
Naxos	428	37.02	25.35	1001	5.8	130	148	36	0	5
Pano Koufonissi	3.8	36.56	25.59	114	0.6	147	15.3	12	0	4
Paros	194.5	37.08	25.12	705	1.6	116	118	8	0	2
Rhodos	1400	36.10	28.00	1215	8.2	21	220	43	4	5
Samos	476.2	37.48	26.44	1434	5.6	2.8	159	14	1	0
Santorin	31	36.24	25.29	586	20.8	173	69	26	1	5
Serifos	73.2	37.11	24.31	585	12	64	81	8	0	0
Sifnos	73.2	36.59	24.4	678	12	87	70	9	0	2
Sikinos	41	36.39	25.06	533	6.6	144	41	8	0	2
Siros	83.6	37.26	24.54	422	16.8	75	87	23	1	2
Skiros	209	38.53	24.32	792	52	75	130	11	0	0
Skopelos	96	39.10	23.40	680	3.2	21	67	7	0	0
Thasos	379	40.41	24.47	1203	57.6	6	95	23	0	0
Tinos	194.3	37.38	25.10	730	8	80	106	13	1	2

are representative of different ecological conditions. Phrygana is the dominant vegetation type throughout the islands, while forest (especially *Quercus coccifera*) and maquis habitats occur only in scattered patches on some of the largest islands. All forests are seriously affected by human activities. Fire and changing grazing pressures create irregular cycles of vegetational change in maquis, so that at one extreme, cover may be less than in most phrygana, while at the other it becomes scrub woodland with a closed canopy. Phrygana is more stable but can be destroyed by burning (Cameron *et al.* 2000). On the Aegean Islands, several tenebrionid species are represented by different subspecies endemic to individual islands or groups of islands. These populations can thus recognised as "evolutionary significant units" (Samways 1998). The current taxonomic dividing line between species and subspecies, as applied to the Aegean tenebrionids, is arguably arbitrary. Most subspecies appear morphologically very close to each other, but usually well recognisable for certain characters. Moreover, there is indication that several populations presently acknowledged as subspecies represent profoundly differentiated populations. For example, a recent taxonomic work on the genus *Dendarus* elevated most of the populations previously considered as subspecies to the status of true species originated as a consequence of a Pleistocene radiation (Chatzimanolis *et al.* 2002, 2003). The exclusion of

subspecies could result in a significant undercounting of endemic island tenebrionid diversity, as species may have been arbitrarily lumped into larger groups. Inclusion of subspecies avoids this problem. For these reasons, following Lewis *et al.* (1998), I have counted populations, presently recognised as subspecies, as different endemic taxa.

Species and subspecies number was used in all analyses, the term 'species' will be used in reference to tenebrionid taxa for simplicity. Data concerning species distribution among islands are the same as in Fattorini (2002a), updated according to Fattorini (2006). As a whole, 170 taxa (138 species and 32 subspecies) were ascertained to occur as native populations on the study islands. I have omitted nine species, cited by various authors from the study islands, because synanthropic, and then possibly introduced, like some species of the genus *Blaps*, associated to ruderal sites, or some cosmopolitan species, such as those of the genera *Alphitobius, Alphitophagus, Tenebrio* and *Tribolium*, strictly associated to human food (Fattorini *et al.* 1999). Since their distribution is profoundly influenced by man, their presence on some islands (usually the most anthropised ones) represent unnatural patterns.

Influence of island characteristics on levels of endemism: The most commonly used estimate of level of endemism in faunal works is simply the percentage of endemic species among all species recorded in a given area. I segregated the recorded tenebrionid species/subspecies into the following three categories: (1) endemic, i. e. taxa endemic to individual islands (endemic at a narrow scale); (2) subendemic, i. e. taxa endemic to groups of islands (endemic at a broad scale); (3) endemic plus subendemic, i. e. taxa endemic to the Aegean archipelago as a whole. To study possible relationships between levels of endemism and island characteristics, I considered the following ecogeographic factors: island's area (A), latitude (La), longitude (Lo), elevation (E), perimeter (P), distance to the mainland (Dm), and distance to the nearest island (Di) (Table I). Latitude and Longitude were converted from degrees and minutes to decimal format using the formula: degrees + (minutes/60).

All geographic variables were Log$_{10}$-transformed to improve normality and reduce heteroscedasticity. Since both log$E$ and log$P$ were tightly correlated with log$A$ (r = 0.874, p < 0.0001 for log$E$ vs log$A$, and r = 0.968, p < 0.0001 for log$P$ vs log$A$), elevation and perimeter were omitted. Along with these variables typically used in island biogeography, I used also some variables describing island shape. The importance of island shape in determining species number has been rarely investigated in island biogeography (Simberloff 1986, Rydin & Borgegärd 1988). To test the importance of island shape on species richness, I used some indexes widely applied in landscape ecology (Farina 1999, Usher & Keiller 1998): Perimeter-Area Ratio ($PARA = P/A$, where P = perimeter, and A = area), Corrected Perimeter-Area Ratio ($CPA = (0.282 * P)/\sqrt{A}$), Related Circumscribing Circle ($RCC = (2*(A/\pi)^{1/2})/\text{longest-axis}$), and Fractal Dimension ($FD = \log P/\log A$). Although FD and $PARA$ deviate from normality, I did not apply transformations to do not mathematically change their primitive significance. I studied the influ-
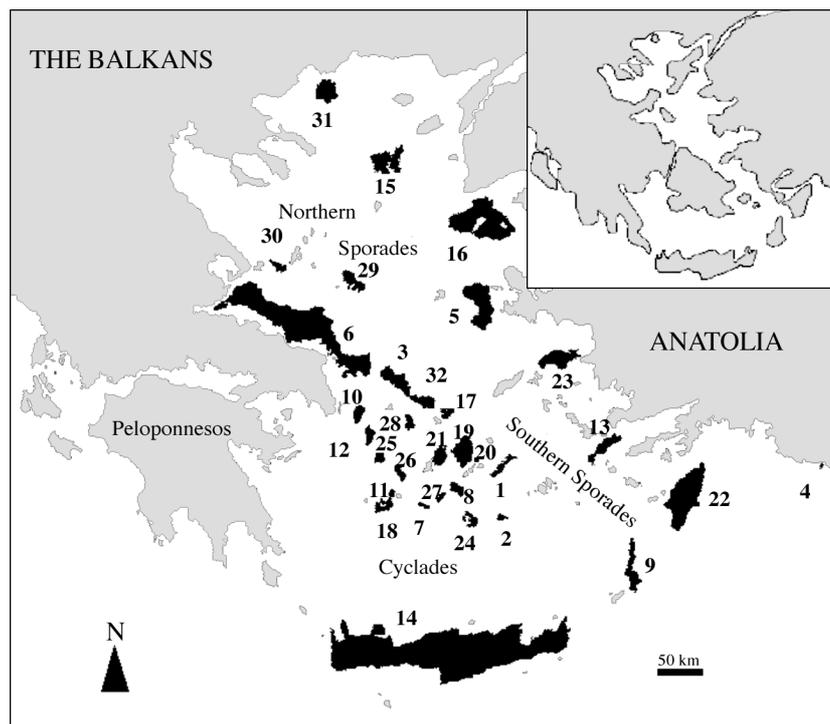
Fig. 1. – Map of the study area. Studied islands are in black. 1: Amorgos, 2: Anafi, 3: Andros, 4: Castellorizon, 5: Chios, 6: Euboea, 7: Folegandros, 8: Ios, 9: Karpathos, 10: Kea, 11: Kimolos, 12: Kithnos, 13: Kos, 14: Kriti, 15: Lemnos, 16: Lesvos, 17: Mikonos, 18: Milos, 19: Naxos, 20: Pano Koufonissi, 21: Paros, 22: Rhodos, 23: Samos, 24: Santorin, 25: Serifos, 26: Sifnos, 27: Sikinos, 28: Siros, 29: Skiros, 30: Skopelos, 31: Thasos, 32: Tinos. Inset: paleogeographic reconstruction of the Aegean area during Pleistocene glacial maximum (modified and combined from Dermitzakis1990, Sfenthourakis 1996, Chatzimanolis *et al.* 2003 and references therein).

ence of both geographic (*A, La, Lo, Dm* and *Di*, all Log$_{10}$-transformed) and shape parameters (*PARA, CPA, RCC* and *FD*) on arcsintransformed proportion values of endemic, subendemic and endemic plus subendemic species by forward stepwise multiple regressions.

Obviously, the actual shape of such multiple relationships cannot be determined on theoretical grounds. However, it is known that logarithmic transformation tend to linearise many monotonic increasing functions (Haila 1983). Thus, it can be postulated that log-transformations increased linearity among eventually curvilinear relationships. For these reasons, I used logtransformed values for many variables even if regressions do not require normality for the independent variables. Here, and in the other analyses described in the following, I preferred to consider geographic and island shape variables as two separate sets, for both logical and statistical reasons. Some geographic parameters are statistically strictly related to some island shape parameters, but have very different biological meanings. Strict correlations among the two set of variables could cause multicolinearity problems in applying stepwise multiple regressions and the importance of a variable of a set could be obscured by a variable of the other set which has a great correlation but a different ecological significance. To assess the impact of multicolinearity on final results, I checked the values of 'tolerance'. As using logtransformed dependent variables the tolerance values of all the variables which entered the models largely exceeded the

threshold value of 0.1 (Hair *et al.* 1998), I believe that the forward stepwise procedure was efficient in selecting variables and results are substantially unaffected by multicolinearity. For purpose of comparison, I also applied pairwise correlations. As results were consistent with those obtained from stepwise regressions, they are not presented.

These analyses were specifically addressed to study if island characteristics may influence the amount of endemism as proportion of species with different degrees of endemism. For comparative purposes I performed analogous analyses using the raw number of endemic (*END*), subendemic (*SUB*), and endemic plus subendemic (*ENS*) species as dependent variables instead of proportions.

Species loss: To calculate the incidence of species extinction in the archipelago, I compared species occurrences on the islands in two time intervals pivoting upon 1960. Species no more recorded in a given island after 1960 were considered extinct in the archipelago. Although this inherently carries with it the loss of some information (number of localities, total number of records, number of specimens), I preferred to use only these data because they are most probably less affected by sampling errors (Turin & Den Boer 1988, Desender & Turin 1989, Maes & Van Dyck 2001). The dividing year (1960) is probably most suitable because the influence of mankind on flora and fauna in Greece, notably on the islands, has never been as strong as during the last forty years (Papanastasis & Kazklis 1998). I used the year 1960 as pivotal date also because it roughly coincides with the publication of Kühnelt (1965) catalogue of the Greek tenebrionids, which is presumably updated to about 1960. Thus, I considered (locally) extinct all species no more collected after 1960 in any examined collection, or no more cited in any published paper after Kühnelt catalogue. Since the Aegean Islands have been repeatedly investigated from 1960 to 2000 (see data and references in Fattorini *et al.* 1999, Leo & Fattorini 2002 and Fattorini & Fowles 2005), I believe that the species not recovered since 1960 are really missing, or at least underwent an extremely high reduction of their local populations.

I referred to collection dates reported in the literature cited by Fattorini *et al.* (1999), Fattorini (2002a), Leo & Fattorini (2002) and Fattorini & Fowles (2005). Necessarily, these assessments reflect the preferences of the original collectors in terms of collection localities, habitats, and species, but they are the best available data. Analogous calculations were performed using 2000 as pivoting date, although in this case estimates of

extinction may be more strongly biased by error sampling.

The following eight species were omitted from these analyses because of lack of information about time of occurrence: *Asida fairmairei graeca, Cylindronotus crenatostriatus, Dichillus pertusus, Erodius orientalis orientalis, Helopelius disgregus, Leichenum pulchellum* cf. *pumilum, Probaticus* sp., and *Stenosis milosana*. Matrixes with temporal data are available as Microsoft Excel files on request.

Relationships between percentage of extinct species and biogeographic categories: To study if the proportion of extinct species varied among distributional ranges, species were classified into the following biogeographic categories (Fattorini 2002a): Widespread (67 species), Balkan (28), Anatolian (16), Endemic (28) and Subendemic (23). To assess whether some biogeographic category was more affected by extinction than expected by its contribution to the total faunal groups, I compared the number of extinct species in each biogeographic category with the number of extinct species expected in each category according to the proportion of each category in the data set using a chi-square goodness-of-fit test. The null-hypothesis was that if there is no biogeographic bias in extinction, each category should have a number of extinct species proportional to its relative importance in the data set. I developed two separate analysis, one dealing with the number of species extinct using 1960 as pivoting data (see above), and the other considering all presumably extinct species in 2000.

Effect of virtual area reduction on endemism: The well-known power function of the species-area relationship has been used successfully to predict extinction rates following habitat loss (Ney-Nifle & Mangel 2000, Zurlini *et al.* 2002, Ulrich & Buszko 2003). If we suppose a reduction of area A_0 to A_1, so that the number of species S_0 is expected to decline to S_1, from the general power function $S = cA^z$, after rearrangements, we obtain $S_1 = S_0 * (A_1/A_0)^z$. The term $(A_1/A_0)^z$ thus represents the proportion of remaining species after area reduction. To be applicable, this equation requires the empirical determination of the z-values according to the power function. Fortunately, the power function fits well with the tenebrionid species on Aegean islands (see below). I applied this function using both the commonly used double logarithmic linearisation ($\log S = \log C + z\log A$) and a curvilinear ($S = cA^z$) fit, because the two equations are not statistically equivalent (Wright 1981) and the 'best fit' in the linearised form curve is biased in favour of points close to the origin of the coordinate system; thus the fact that 'a best' fit was found between $\log A$ and $\log S$ does not imply that one obtains the 'best fit' between A and S (Pattyn & van Huele 1998). On the other hand, in a curvilinear regression, the parameter estimates may be too heavily influenced by large values, causing shortcomings in the use of this technique (Welter-Schultes & Williams 1999), and the double logarithmic linearisation is usually applied to estimate species loss after habitat loss (Zurlini *et al.* 2002, Ulrich & Buszko 2003, Ulrich 2005). For these reasons, I applied and compared both models.

According to Ekbohm & Rydin (1990), the usual R^2 statistic

can be used to compare the two models, although based on Y-transformation, because R^2 is dimensionless and the two models have the same number of parameters. To compare curvilinear and linearised models based on different numbers of parameters, these authors proposed to use the adjusted coefficient of determination (Ra^2), $Ra^2 = 1 - (1 - R^2)(n - 1)/(n - k)$, where n is the number of islands, and k is the number of parameters in a model.

By contrast, according to other authors (Kvålseth 1985), the R^2 statistic is problematic for comparing models based on different transformations of the Y-axis, because the R^2 computed from log-transformed variables holds only for the linearised space obtained by the transformation and cannot be compared with the R^2 computed from the untransformed data. Kvålseth (1985) suggests computing an alternative R^2 here called *FI* (fit index) according to the equation: $FI = 1 - (RSS/TSS)$, where:

$$TSS = \sum_{i=1}^{n}(Y_i - \overline{Y})^2 \ , \ \ RSS = \sum_{i=1}^{n}(Y_i - \hat{Y}_i)^2$$

In *TSS* and *RSS* calculations $\hat{Y}_i$ is the backtransformed value of the estimated Y in the transformed space and $\overline{Y}$ is the mean of the backtransformed data. When a logarithmic estimate is backtransformed into original units it is biased downward because the antilogarithm of the estimated mean gives the geometric rather than the arithmetic mean. To account for this bias, antilogs of species richness calculated from regressions can be corrected by multiplying the antilogs by e^c, where $c = 2.65 * S_{yx}^2$ and S_{yx} = standard error of estimate in Log_{10} units (Ferguson 1986). This statistic can be compared to the R^2 computed from the curvilinear fit, calculated as $R^2 = 1 - (SSE/SST)$, where *SSE* is the sum of the squared residuals and *SST* is sum of the squared Y values minus the mean sum of squares.

Models were also compared using the 'root mean-square deviation' (Δ), i. e. the square root of the *RSS* divided by the number of samples (He & Legendre 1996).

The z-values obtained by these two models were used to calculate the term $(A_1/A_0)^z$ after a reduction of 50%, 66.6%, and 75% of original area size. Although there was obviously no actual area size reduction in the Aegean Islands, this analysis allows comparing the percentages of extinct species with those that one could estimate by a virtual dramatic reduction in area size if islands were patches of a fragmented landscape.

I applied the same procedure to the endemic species, the subendemic species and the endemic plus subendemic species. On the basis of fits statistics, biological appropriateness of values of fitted parameters and visual inspection of scatterplots, the only realistic model was that obtained between number of endemic species and area after double logtransformation. As in similar works (Kerr 1997, Zurlini *et al.* 2002), $\log(x + 1)$ transformation was used to avoid undefined values for islands with no endemic. This line was also compared to a regression line constructed for nonendemic species.

Effect of distance on species richness: Most of the Aegean Islands were connected to one another and/or to the mainland during the last ice age (Fattorini 2002a). Thus, they were avail-

able to colonisation by land-bridge mechanisms. Because the species-area relationship is a consistent phenomenon, the best way to consider other sources of variation in species number is through the analysis of residuals (deviations) from species-area regressions (e. g. Price 2004). If present species richness is influenced by present immigration, a negative influence of island distance from the mainland and/or of inter island distance on species richness is expected. I have therefore correlated the residuals of the aforementioned species-area relationships to logtransformed Dm and Di. Scatterplots were examined to assess the potential for nonlinear or unimodal relationships between residuals and distances. As the influence of distance on the total richness could be obscured by the presence of endemics (i. e. taxa not truly coming from the mainland but evolved *in situ*), the possible influence of distance is expected to be clearer if the analysis is restricted to the species occurring in mainland areas. Thus, I performed the same analyses on the 'mainland' species alone (i. e. $S - ENS$).

Comparisons of tenebrionid level of endemism with other groups: The incidence of endemic species among tenebrionids was compared with the levels of endemics recorded for other invertebrate groups in the Aegean archipelago for which detailed data are available: terrestrial molluscs and isopods (Sfenthourakis *et al.* 1999), centipedes (Zapparoli 2002), snakeflies (Aspöck 1979), blister beetles (Bologna & Marangoni 1990) and butterflies (Dennis *et al.* 2000). To test whether the proportion of endemic taxa was statistically different between tenebrionids and each of the aforementioned groups, I used the formula (Zar 1984):

$$Z = \frac{P_1 - P_2}{\sqrt{P(1-P)\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

where: $P1$ = proportion of endemic tenebrionids, $P2$ = proportion of endemic taxa belonging to another group, n_1 = total number of tenebrionids, n_2 = total number of taxa belonging to the other group,

$$\text{and } P = \frac{n_1 P_1 + n_2 P_2}{n_1 + n_2}$$

The null hypothesis H_0: $P_1 = P_2$ is rejected if $Z < -Z_\alpha$ or $Z > Z_\alpha$. For p = 0.05, $Z_\alpha = t_{0.05(2)} = 1.960$ (and for p = 0.01, $Z_\alpha = 2.576$, for p = 0.001, $Z_\alpha = 3.291$).

Analyses were performed using STATISTICA software (version 4.5, 1993). In all aforementioned tests, a minimum probability level of p < 0.05 was accepted (all tests were two-tailed). I made many tests on the same data set, thereby increasing risk of significant results occurring by chance. Although the sequential Bonferroni has become the standard method of dealing with multiple statistical tests, I believe, that decreasing the significance level would have resulted in an even higher risk of ignoring real relationships. Moran (2003) showed that the sequential Bonferroni has several flaws ranging from mathematical (it ignores the number of statistical tests that are significant) to log-

Table II. – Stepwise multiple regressions between levels of endemism and island's characteristics. Only significant variables are reported. A = area (Km^2), La = latitude (decimal degrees), Lo = longitude (decimal degrees), Di = distance to the nearest island (Km), Dm = distance to the nearest mainland (Km), RCC = Related Circumscribing Circle. β = standardised regression coefficient (weight); B = non-standardised regression coefficient. SE = standard error; SEE = Standard error of estimate. Regression results: (1) $R^2 = 0.322$, $R^2_a = 0.222$, $F_{(4,27)} = 3.209$, p < 0.05, SEE = 7.979; (2) $R^2 = 0.617$, $R^2_a = 0.560$, $F_{(4,27)} = 10.879$, p < 0.0001, SEE = 9.080; (3) $R^2 = 0.583$, $R^2_a = 0.539$, $F_{(3,28)} = 13.067$, p < 0.0001, SEE = 8.803; (4) $R^2 = 0.602$, $R^2_a = 0.543$, $F_{(4,27)} = 10.205$, p < 0.001, SEE = 2.401; (5) $R^2 = 0.576$, $R^2_a = 0.513$, $F_{(4,27)} = 9.171$, p < 0.0001, SEE = 1.337; (6) $R^2 = 0.618$, $R^2_a = 0.561$, $F_{(4,27)} = 10.911$, p < 0.0001, SEE = 3.204; (7) $R^2 = 0.123$, $R^2_a = 0.094$, $F_{(1,30)} = 4.198$, p = 0.049, SEE = 4.604. All independent geographic variables are Log_{10}-transformed; proportions were arcsintransformed. Regression seven is the only one for shape parameters which was significant.

	β	SE β	B	SE B	p-level
			Proportions		
%END (1)					
Intercept			540.286	183.437	0.007
La	-0.519	0.176	-344.304	116.615	0.006
%SUB (2)					
Intercept			218.380	338.701	0.525
Dm	0.485	0.144	9.868	2.932	0.002
Di	-0.321	0.131	-9.308	3.796	0.021
%ENS (3)					
Intercept			927.370	201.379	<0.0001
La	-0.606	0.134	-576.513	127.542	<0.0001
			Raw numbers		
END (4)					
Intercept			344.931	77.410	<0.0001
A	0.572	0.127	2.883	0.638	<0.0001
La	-0.691	0.142	-180.091	37.020	<0.0001
Di	0.363	0.134	2.725	1.005	0.011
Lo	-0.288	0.137	-49.710	23.633	0.045
SUB (5)					
Intercept			86.800	47.971	0.082
La	-0.505	0.157	-71.068	22.020	0.003
A	0.407	0.138	1.106	0.376	0.007
Dm	0.430	0.161	1.224	0.457	0.012
ENS (6)					
Intercept			331.927	73.647	<0.0001
La	-0.616	0.132	-218.470	46.819	<0.0001
A	0.616	0.129	4.227	0.888	<0.0001
ENS (7)					
Intercept			11.123	4.062	0.010
RCC	-0.350	0.171	-14.223	6.942	0.049

ical (there is no standard way to apply the test) to practical (e. g. the probability of finding a significant result declines in more detailed studies). Thus, in accordance with the suggestions of Moran (2003), I did not apply the Bonferroni correction, but focused on p-values and consistence of results.

RESULTS

Influence of island characteristics on levels of endemism

Table II reports results obtained by arcsintransformed proportions and raw numbers. As to the percentage of endemic taxa, only latitude showed a significant (negative) correlation in the stepwise regression. The correlation between endemics and latitude is probably because of the high number of endemic taxa occurring on Kriti and Rhodos. As to the percentage of subendemic taxa, distance to the mainland (positively) and distance to the nearest island (negatively) entered significantly the stepwise regression. Finally, the percentage of endemics plus subendemics was significantly negatively affected by latitude. With regard to the shape variables, none of them significantly contributed to multiple regressions models developed for arcisntransformed percentage of endemics, subendemics and endemics plus subendemics.

Forward stepwise regression of *END* on the geographic variables revealed a significantly positive influence of area and distance to the nearest island, and a significantly negative influence of latitude and longitude. *SUB* was positively affected by both area and distance to mainland, and negatively by latitude. Finally, *ENS* was negatively affected by latitude and positively by area. A forward stepwise regression with shape variables gave a significant model only for *ENS*, which appeared negatively affected by *RCC*.

Species loss and relationships between percentage of extinct species and biogeographic categories

Extinct species were 27% before 1960 (3% as Anatolian, 6 % as Balkan, 6 % as Endemic, 2 % as Subendemic, and 10% as Widely distributed) and 59% until 2000 (6% as Anatolian, 9% as Balkan, 12% as Endemic, 9% as Subendemic, and 23% as Widely distributed). The high proportion of extinct widely distributed species may be simply a reflection of the predominance of this biogeographic category in the data set. Actually, for both pivoting dates, the observed numbers of extinct species for the different biogeographic categories were not different from those expected from the general frequencies of the categories in the data set ($\chi_{(4)}^2 = 2.875$, p = 0.579 and $\chi_{(4)}^2 = 0.864$, p = 0.930 for 1960 and 2000 respectively). Thus, species become extinct in each category with the same frequency of each category in the total fauna.

Effect of virtual area reduction on endemism

The power function, applied after linearisation, gave the model: $\log S = 0.529 + 0.260 \log A$ ($R^2 = 0.359$, *FI* = 0.514, $Ra^2 = 0.338$; $\Delta = 9.527$). A curvilinear fit gave the
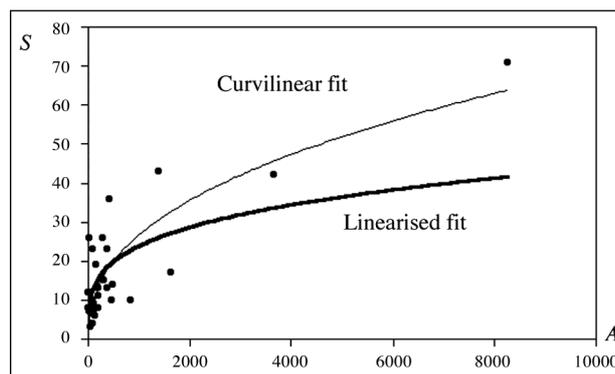
Fig. 2. – Species (*S*) -area (*A*) relationship based on linearised and curvilinear fits for the power function model.

model: $S = 1.547A^{0.412}$ ($R^2 = 0.660$, $Ra^2 = 0.648$; $\Delta = 8.198$). Use of the power function by curvilinear regression gave a higher R^2 and Ra^2 than the linearised form does. The *z*-value of 0.260 obtained from the power function in its linear form is however very close to that (0.263) predicted by theory (e. g. Sugihara 1981). By contrast, the *z*-value obtained by the curvilinear fit was substantial higher ($z = 0.41$), possibly a reflection of the stronger influence of higher values.

Using $z = 0.26$, when 50%, 63.3% and 75% of island area is virtually eliminated, the amount of remaining species is 83.5%, 75.1% and 69.7% respectively. If $z = 0.41$ is used, species decline more sharply, and the amount of remaining species is 75.2%, 63.7% and 56.6% respectively. These values can be compared with the species known as living at the two pivoting dates 1960 and 2000. In 1960, about 73.5% of the original fauna was present, while in 2000 only 42% could be ascertained to be present. Thus, the percentage of species extinct before 1960 is roughly the same as expected after area was virtually reduced to 50-63%, while the percentage of species extinct before 2000 greatly exceeded the percentage expected after area was reduced of 75%. In particular, an amount of remaining species of 73.5% (1960) should correspond to a virtual reduction of about 53% ($z = 0.41$) to 69% ($z = 0.26$) of island area, while an amount of 42% (2000) should correspond to a virtual reduction of about 87% ($z = 0.41$) to 98% ($z = 0.26$) of island area.

Obviously, there was no real area size reduction in the Aegean Islands, but these figures clearly show that the percentages of extinct species equal or greatly exceed those that one could estimate by hypothetical dramatic reductions in area size.

As to the endemic species, I obtained the model: $\log(END + 1) = -0.259 + 0.183 \log A$. Using this $z = 0.183$, when 50%, 63.3% and 75% of the island area is virtually eliminated, the amount of remaining endemic species is 88.1%, 81.8% and 77.6% respectively. A curvilinear fit gave the unrealistic model: $END = (9.683*10^{-11})A^{0.289}$ where the extremely low *C* values is probably due to the high number of islands with zero values. However, using this

$z = 0.289$, when 50%, 63.3% and 75% of the island area is virtually eliminated, the amount of remaining endemic species is 81.9%, 72.8% and 67% respectively. For the non endemic species, I obtained the model: $\log(S\text{-}END) = 0.526 + 0.260\log A$, which has the same z as the general model. The regression line for endemic species appears below than that found for the entire data set or for the non endemic species. Thus, islands, and especially small islands, appear more effective in capturing species richness than endemic species. As area increases, the number of endemic species increases, but the number of non-endemics increases far more (larger z); therefore, an island is expected to contain a large number of species even if it has few or no endemic species and if it is very large.

Effect of distance on species richness

Residuals of the aforementioned linearised power function were not correlated to distances to either the mainland ($\log Dm$ r = -0.017, p = 0.928) or the nearest neighbouring island ($\log Di$ r = 0.115, p = 0.532). Use of residuals from the curvilinear model gave identical outcomes. The analyses restricted to the species occurring on mainland areas gave equations very similar to those discussed above and no correlations were found between distances and residuals. Consequently, rather than being influenced by the extent of island isolation from the mainland or adjacent islands, tenebrionid communities on these land-bridge islands area determined by island history and the initial set of species occurring on the island prior to isolation (see also Fattorini 2002a).

Comparisons of tenebrionid level of endemism with other groups

The percentage of endemic tenebrionids in the Aegean archipelago (*ca* 32%) greatly exceeds that of centipedes (*ca* 14%, Z = 2.944, p < 0.01), butterflies (*ca* 5.2%, Z = 5.908, p < 0.001) and blister beetles (6%, Z = 3.795, p < 0.001). By contrast, it appears similar to that of snake-flies (*ca* 38%, Z = -0.526, p > 0.05), and isopods (*ca* 33%, Z = -0.284, p > 0.05). Finally, it is inferior to that of molluscs (*ca* 48%, Z = -5.959, p < 0.001).

DISCUSSION

For the Aegean Islands levels of endemism appear poorly influenced by present geography or island shape. In particular, the proportion of endemic taxa appears uncorrelated with island present isolation, while the proportion of subendemic taxa appears to be affected by present distance to the mainland and inter-island distance. These results can be interpreted taking into account the relictual character of the Aegean tenebrionid fauna.

The Aegean tenebrionids constitute a non-equilibrial fauna (Fattorini 2002a) and their present distribution is a result of past (Pleistocene) colonisation by land-bridge dispersal, eventually followed by vicariance and, hence, allopatric speciation (Fattorini 2002b, 2006, Hausdorf & Hennig 2005). During the Pleistocene lowering of the sea level, most of the remote islands were mutually connected, forming various Pleistocene groups of islands. These enlarged Pleistocene island groupings were however separated to one another, allowing for the evolution of taxa that are presently restricted to the islands which formed the same Pleistocene group (i. e. subendemic taxa) (see biogeographic analyses presented by Fattorini 2002a). As shown by paleogeographic reconstructions, these various Pleistocene island groupings were presumably located at different distance to the mainland, accounting for a positive correlation between proportion of subendemic taxa and distance to the mainland. Such Pleistocene island groupings were represented by islands which are also presently very close to one another, allowing for a negative relationship between the percentage of subendemic taxa and the inter-island distance. Only few islands were completely isolated, evolving strictly endemic taxa (Fattorini *et al.* 2000). As this isolation was probably not related with the distance to the mainland, the proportion of endemics appears presently uncorrelated with distance.

As with the raw number of species, latitude negatively affected *END, SUB* and *ENS*, which may be a possible reflection of increasing areas at lower latitudes, or a greater persistence of species during Pleistocene glacials, because of a more suitable climate in southern islands. The increasing number of species with area falls within the well-known positive relationships between species and area

On the whole, the Aegean tenebrionids show a high percentage of taxa endemic to the Archipelago (*ca* 32%). This strongly contrasts with the incidence of endemic taxa in centipedes, butterflies, and blister beetles, as a result of their different dispersal ability and biogeographic history. Tenebrionid beetles are strictly resident organisms which colonised the Aegean Islands by means of Pleistocene land-bridges, whilst present overwater dispersal from mainland or among islands may have only a secondary role in determining distribution patterns (Fattorini 2002a, 2002b).

Let us remark that the Aegean flightless tenebrionid species also occur in the adjacent mainland areas (i. e. Greece and Anatolia) or, if endemic, belong to flightless genera (Fattorini *et al.* 1999). Therefore, flightlessness in Aegean tenebrionids evolved before island colonisation, and it is not a consequence of living on islands. According to Brühl (1997), passive long distance transport and active dispersal is very improbable in insects which are large and lack wings. Even though some tenebrionid species have been known to colonise islands over substantial distance of water, most of these dispersal events

occurred over very long periods of time (millions of years cf. Palmer 1998). Thus, it is unlikely that recolonisation has been common over the relatively brief period since the last ice age. Several lines of evidence suggest that recolonisation is not an important factor in determining the present distribution of the tenebrionids of the Aegean Islands. First, if recolonisation were an important process determining the tenebrionid communities on the islands, one would expect islands closer to the mainland to harbour, on average, more species. However, no statistically significant relationship exists between the number of species occurring on an island and its distance to the nearest neighbouring island or to the mainland after the effect of island area has been removed. Geographic barriers imposed by large water gaps clearly affect dispersal in flightless beetles, although drift and vegetation may be vehicles for many heavy-body insects and adjacent down-current islands are the most favourable for the arrival of drifting beetles. However, a study made by Howden (1977) on the beetles occurring in beach drift, revealed that, in contrast with carabid beetles, which were represented by several living individuals belonging to many species, tenebrionids were represented by few individuals, sometimes dead, and belonging to very few species. Also, floating vegetation mats are almost absent in the arid environment of the Aegean Islands. Finally, most tenebrionids are too large to be easily transported by wing, while human mediated dispersal has to be discarded because anthropophilic species were preventively omitted from the analysis. On the basis of the colonisation wave of Canarian species for which colonisation times based on genetic analyses are available, Palmer (1998) carefully evaluated the probability that wingless tenebrionids have to colonise islands by sea dispersal: this probability was negligible, thus sea dispersal can occur, but only as a very rare case. Little is known about the ability of tenebrionids to survive or remain afloat in salt water, although one study showed that beetles remained afloat and alive in the Baltic Sea for 5 days (Palmen 1944). By contrast, centipedes have an extraordinary over-sea dispersal ability, being able to survive also for some months submerged in salt water (Foddai *et al.* 1996). Likewise, butterflies are mobile organism, capable of crossing extensive sea barriers (Dennis *et al.* 2000). Blister beetles also have a high dispersal power, because their larvae are transported by bees and grasshoppers (Bologna & Marangoni 1990). Thus, all these invertebrates tend to constitute equilibrial faunas, usually preventing allopatric speciation by inter-island isolation, as conversely supposed for tenebrionids. By contrast, both snake-flies and isopods have comparable endemism levels. Actually, snake-flies are known to be very poor fliers, and terrestrial isopods are usually strictly associated to litter, being thus poorer colonisers. Finally, terrestrial molluscs, strictly dependent on litter and calcareous substrates, show an even higher endemism per-

centage than tenebrionids do, thus suggesting that taxa with lower mobility are subject to more allopatric speciation rate as a consequence of their reduced inter-population genetic flow.

Most of the islands possess few tenebrionid endemics, usually belonging to different genera, while sharing higher numbers of subendemics. Thus, while the percentage of subendemic species on each island can be high, as a consequence of the fact that such islands were parts of the same Pleistocene island groupings, the percentage of strictly endemic is very low. The most relevant exception is Kriti (Crete), which harbours a great number of strictly endemic taxa (28%), with several subspecies of the same tenebrionid species. Allopatric speciation within a small area is unlikely, while on Kriti, which is the largest island, several events of allopatric speciation occurred, resulting in a high number of conspecific tenebrionid taxa, and this pattern is paralleled by several taxa (Legakis & Kypriotakis 1994). 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. These Cretan paleoislands were joined only in the Pliocene (3-2 Ma). This long isolation time allowed the species populations on the paleoislands to diverge sufficiently to become different taxa (Legakis & Kypriotakis 1994, Welter-Schultes & Williams 1996, Welter-Schultes 2001). According to Legakis & Kypriotakis (1994) when the island was reunited, the animal populations, not being very abundant, remained in their original distribution areas without having to compete with each other and with other populations from outside Kriti. If reduced competition among low density populations determined the survival of strictly related taxa in adjacent areas, it can be expected that sedentary animals, being confined to the original areas, where less subject to competition than more vagile ones, which interact when expanding their range. In other words, in the relatively reduced area of this island, endemism should be enhanced in the most sedentary animals as a consequence of both the reduced genetic flow among populations and the low competitive interactions. Interestingly, the high incidence of Cretan tenebrionid endemics largely exceeds those of plants (12%) and butterflies (a mere 7%), but it is comparable with that of other sedentary animals, like molluscs (50%) (Dennis *et al.* 2000, and references therein). However, lack of data on the density of population makes not possible to completely assess the correctness of Legakis & Kypriotakis model.

Ecological theory assumes that endemic species are most prone to extinction, thus deserving special attention in conservation biology. Considering the whole archipelago as if it was an assemblage of patches of a fragmented landscape, it is possible to calculate the percentage of extinct species out of the original whole assemblage by area reduction (habitat loss) using the species-area relationship with appropriate slope. Extinction estimates gen-

erated by species-area relationship models for fragmented landscapes and preserves networks usually tend to be greater than observed extinction, because they are not based on the number of species confined to the destroyed habitat but on the total number of species present here (Zurlini *et al.* 2002). Rather surprisingly, the number of extinct species observed in the study area exceeded largely those which a model could predict even for a disproportionate amount of area (habitat) loss. Aegean islands obviously do not change their area size from the end of the nineteen century to present time, neither they loss natural habitat at so large levels as those expressed by the degree of area reduction introduced in the models. Thus, on the Aegean Islands tenebrionid extinction occurred with a dramatic rate, largely exceeding that expected from a disproportionate loss of habitat.

This worse scenario may result from the high incidence of geographically restricted (endemic and subendemic), and hence likely numerically rare, species, and from their low dispersal ability, a combination of traits which makes the Aegean tenebrionids extremely prone to extinction.

The emerging view regarding population viability analysis (PVA) is that demographic and environmental stochasticity can increase the likelihood of population extinction for rare species, particularly in small areas where they are more vulnerable (Zurlini *et al.* 2002). Endemic species – that are thought of as rare because they have small ranges – are limited by colonisation ability. This does not necessarily mean that these species are poorer colonists than abundant species. Historical factors to be considered are recent speciation or past environmental conditions. These conditions could indicate that the species has had less time to spread into areas which they have the capacity to occupy at the present time. However, when species are relicts of former faunas and have low dispersal ability, they cannot spread outside present ranges. Flightlessness considerably reduces the beetles' ability to actively disperse. Turin & Den Boer (1988) demonstrated that poorly dispersing beetles generally show decreasing time trends, and Den Boer (1990) pointed up that the local populations confined to small localities without replacement are eventually likely to become extinct. As Aegean tenebrionids are *per se* typically restricted to small areas and have low dispersal power, they are inherently highly vulnerable, allowing for the astonishing observed high rate of extinction.

According to Cook & MacDonald (2001), endemism should be defined by three primary attributes: taxonomic validity, spatial scale and temporal scale. With regard to the taxonomic validity, most of the endemic tenebrionid taxa are represented by populations presently recognised as subspecies and could simply be the result of the overzealous taxonomic splitting of the entomological work in the earlier part of nineteen century. In fact, there is indication that most of the populations presently acknowledged as subspecies represent actually differentiated populations, possibly even more than their subspecific rank implies (Chatzimanolis *et al.* 2002). Failure to recognise and conserve these distinct lineages may lead to serious management mistakes (Cook & MacDonald 2001). With regard to the spatial scale, after several decades of intensive research, we can suppose that our information on spatial distribution is accurate enough. Thus, it is rather unlikely that populations recognised as endemic are distributed outside their known range. Finally, we can make up some discussion about the temporal scale of the endemic tenebrionid taxa. Myers & De Grave (2000) criticised distinguishing paleoendemics (i. e. older, relictual lineages that once had larger distributions) from neoendemics (i. e. newer lineages that are the result of recent arrival and *in situ* differentiation), while they proposed to distinguish between cryptoendemics (extinction mediated endemics) from euendemics (which never had a significantly wider range). Although a lack of reliable phylogenetic analyses makes it difficult to apply these concepts to the Aegean tenebrionids, most of the endemic tenebrionids could be contemporarily regarded as paleoendemics and euendemics. Their actual distribution does not derive from range contractions (as for cryptoendemics), but they evolved on the single islands by allopatric mechanisms, as a result of the fragmentation and isolation of ancestral populations distributed over larger areas (paleoendemics). This peculiar status of paleo-euendemics makes these taxa of highest conservation interest, because taxa with longer history of divergence should be accorded higher conservation protection in the perspective of maintaining the evolutionary potential of the biota (Cook & MacDonald 2001).

CONCLUSIONS

This research highlights the importance of historical determinants of present community structure in a non-equilibrial archipelago and the incidence of low mobility in increasing speciation. Levels of endemism in the Aegean tenebrionids appeared poorly influenced by present geography or island shape, while past land configurations appeared to have a major role, as expected for flightless beetles, which are more affected by past vicariance and/or dispersal events than present dispersal. Flightless beetles presumably colonised the Aegean islands mostly by means of Pleistocene land-bridges. When the sea level was restored, island populations remained isolated from the mainland ones, becoming endemic to single islands or island groups. Extinction events observed in the study area exceeded largely those which a model based on the species-area relationship could predict even for a disproportionate amount of area (habitat) loss, possibly as a consequence of the particular relict condition of the Aegean fauna. In equilibrial faunas,

extinct species can be replaced by new colonists. In non-equilibrial islands, niches left empty by extinct species (which colonised the island by past land-bridges) cannot be occupied by new colonists, because islands are now almost inaccessible to colonisation. In other words, flightless tenebrionids mostly colonised the Aegean islands when they were connected to one another or to the mainland. When such a species disappears on an island, no other tenebrionid species can occupy its niche coming from the mainland because of their low ability to over-sea dispersal. As a result, relict faunas are extremely fragile and deserve special attention in conservation biology because of both the high incidence of endemics and the irreplaceability of most species.

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