

Levels of endemism in the Aegean Tenebrionids (Coleoptera, Tenebrionidae)¹

SIMONE FATTORINI*, PIERO LEO**, LUCA SALVATI***

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

***Via P. Tola, 21 - I-09128 Cagliari (Italy)*

****Piazza F. Morosini, 12 - I-00136 Rome (Italy)*

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SUMMARY

This paper is based on the distributions of native tenebrionid species and subspecies on 33 islands in the Aegean Sea. On a total of 166 tenebrionid taxa recorded from the studied islands, 37 (22%) are considered endemic (*i.e.*, taxa restricted to a single island), and 23 (14%) subendemic (*i.e.*, taxa occurring on more than one island but not on the mainland). Percentage of endemic taxa was positively correlated with island area, while percentage of subendemic taxa was negatively correlated with area and positively with distance to the mainland. These different patterns could be related to palaeogeographical scenarios. Subendemic taxa probably evolved on islands that, during Pleistocene, were mutually connected forming various island groups presumably at different distances to the mainland, while endemic taxa generally evolved on islands that were completely isolated also in Pleistocene. As a rule, islands that were connected to the mainland during Pleistocene regressions show low levels of endemism, while islands that were never connected to the mainland show generally higher levels of endemism.

INTRODUCTION

Levels of faunal endemism have been considered in basic researches (*e.g.*, Anderson, 1994) as well as in works concerning biodiversity conservation (*e.g.*, Oosterbroek, 1994). The commonly adopted evaluation of the level of faunal endemism is the percentage of endemic taxa among all taxa recorded within a given area. However, considerable debate still surrounds the definition of

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endemism. According to Zunino and Zullini (1995), endemism is not linked to the size of the area but corresponds to the exclusive occurrence of a taxon in that area. On the other hand, a taxon is generally considered as endemic when its geographical distribution is restricted to a small area (Horton, 1973). However, this definition depends on the spatial scale considered, because the size of the distribution area of a taxon depends on the size of the considered geographical area (Udvardy, 1969; Peterson and Watson, 1998). Also, the number of taxa considered to be endemic to an area largely depends on taxonomic concepts of the students: lumpers are inclined to consider only those taxa that are very well characterized and separated from all other relatives, while splitters are inclined to consider even little different local populations to be endemic taxa.

As to insular endemics, a taxon occurring on only one island is obviously endemic to that island. In addition, there are taxa occurring on various islands within a given archipelago but absent from other islands of the same archipelago: these taxa can be considered as subendemic to the islands and endemic to the archipelago.

From an evolutionary viewpoint, all insular populations will evolve away from the one another and from the mother population. Of course, many insular populations are indistinguishable from others due to their relatively youthfulness. According to Mac Arthur and Wilson (1967), youthfulness in members of an equilibrium fauna implies extinction of other, former members and the percentage of non-endemic taxa should be a measure of the turnover rate; because the turnover rate varies inversely with island area, percentage of endemism should increase with island area.

The aim of this paper was to evaluate which factors could have caused differences in the percentage of endemic tenebrionids among Aegean Islands.

MATERIAL AND METHODS

A total of 33 faunistically well known Aegean Islands was included in this study (Fig. 1, Tab. I). On the Aegean Islands, several species are represented by different subspecies on individual islands or groups of islands. However, it is difficult, at present, to state the actual taxonomic status of many insular populations because of lack of large systematic reviews. In particular, some insular populations recognized as subspecies could be actually not differentiated. In case of doubtful subspecies, we have considered only the species level. By contrast, other insular populations, presently recognized as subspecies, appear to be well separated and could be true species. We have counted these populations as separated taxa. Therefore, we have included in this study both species and subspecies, for a total of 166 taxa. Figures reported in Tab. I are based on accepted literature data and material examined by the authors. Examination of tenebrionid collections maintained at Museo di Zoologia, Università di Roma

“La Sapienza” revealed many new island tenebrionid records and confirmed most of the literature data. Specimens preserved in P. Leo’s and C. Meloni’s collections (Cagliari) provided other data, including some new records. Let us remark that we have omitted various species, cited from the study islands, because synanthropic, transient, exotic or of uncertain distribution. A detailed account of all recorded species (including the new records), as well as criteria used to reject data, are reported in another work (Fattorini et al., 1999).

The variables used as evaluation of endemism were: (i) number of endemics (END: *i.e.*, species and subspecies restricted to a single Aegean island), (ii) number of subendemics (SUB: *i.e.*, species and subspecies occurring on more than one island within the Aegean area but not on continents or elsewhere), (iii) number of endemics and subendemics (ENS: *i.e.*, END + SUB), (iv) percentage of endemics (%END), (v) percentage of subendemics (%SUB), and (vi)

Tab. I - Number of species and subspecies recorded on each island. TOT = Total number of species and subspecies; END = Number of endemic species and subspecies; SUB = Number of subendemic species and subspecies; ENS = Number of endemic and subendemic species and subspecies.

Island	TOT	END	SUB	ENS	%END	%SUB	%ENS
Amorgos	7	0	2	2	0.0	28.6	28.6
Anafi	11	0	4	4	0.0	36.4	36.4
Andros	11	1	3	4	9.1	27.3	36.4
Armathia	4	0	3	3	0.0	75.0	75.0
Castellorizon	7	1	0	1	14.3	0.0	14.3
Chios	10	0	1	1	0.0	10.0	10.0
Euboea	40	1	0	1	2.5	0.0	2.5
Folegandros	3	0	1	1	0.0	33.3	33.3
Ios	9	0	2	2	0.0	22.2	22.2
Karpathos	13	0	3	3	0.0	23.1	23.1
Kea	6	1	1	2	16.7	16.7	33.3
Kimolos	3	0	1	1	0.0	33.3	33.3
Kithnos	4	0	0	0	0.0	0.0	0.0
Kos	21	0	3	3	0.0	14.3	14.3
Kriti	70	22	7	29	31.4	10.0	41.4
Lemnos	10	0	0	0	0.0	0.0	0.0
Lesvos	16	0	1	1	0.0	6.3	6.3
Mikonos	10	0	5	5	0.0	50.0	50.0
Milos	19	1	4	5	5.3	21.1	26.3
Naxos	37	0	7	7	0.0	18.9	18.9
Paros	8	0	3	3	0.0	37.5	37.5
Rhodos	39	5	5	10	12.8	12.8	25.6
Samos	13	2	0	2	15.4	0.0	15.4
Santorin	26	1	6	7	3.8	23.1	26.9
Serifos	7	0	0	0	0.0	0.0	0.0
Sifnos	9	0	2	2	0.0	22.2	22.2
Sikinos	7	1	2	3	14.3	28.6	42.9
Sirna	2	0	1	1	0.0	50.0	50.0
Siros	22	1	3	4	4.5	13.6	18.2
Skiros	10	0	0	0	0.0	0.0	0.0
Skopelos	7	0	0	0	0.0	0.0	0.0
Thasos	13	0	1	1	0.0	7.7	7.7
Tinos	13	1	3	4	7.7	23.1	30.8

percentage of endemics and subendemics (%ENS). %ENS was used as an evaluation of the level of total endemism. Mean±S.D. of %ENS was calculated and used to group islands into two classes: islands with %ENS lower than mean %ENS, and islands with %ENS higher than mean %ENS. Island areas and distances to mainland were calculated on 1: 800000 and 1: 2500000 maps.

To study the relation between number of taxa and area, three different mathematical models were used: the linear function, the exponential function, and the power function.

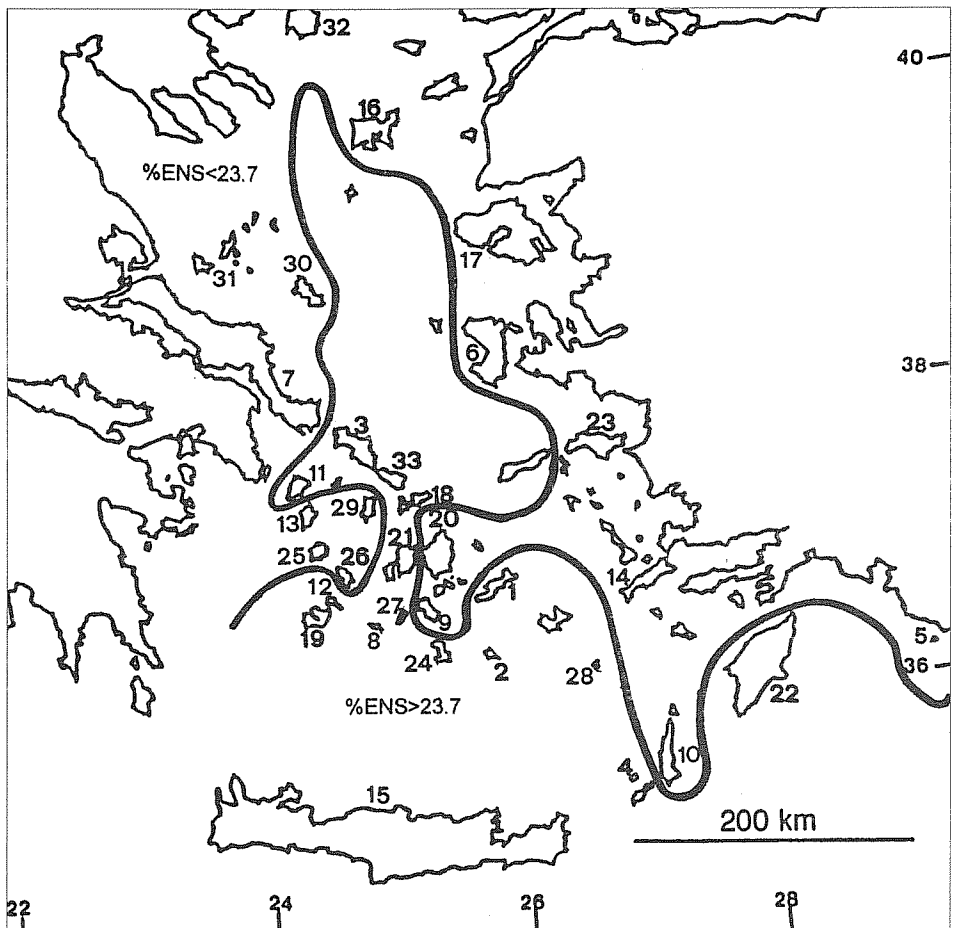


Fig. 1. Map of the study area. Island names follow Strid (1970) and other commonly used versions. 1 Amorgos, 2 Anafi, 3 Andros, 4 Armathia, 5 Castellorizon (= Megisti, Kastelorizo), 6 Chios (= Hios, Kios), 7 Euboea (= Evvia, Evvoia), 8 Folegandros, 9 Ios, 10 Karpathos, 11 Kea, 12 Kimolos, 13 Kithnos, 14 Kos, 15 Kriti (= Crete), 16 Lemnos (= Limnos), 17 Lesvos, 18 Mikonos, 19 Milos, 20 Naxos, 21 Paros, 22 Rhodos (= Rodos, Rhodes), 23 Samos, 24 Santorin (= Thira, Santorini), 25 Serifos, 26 Sifnos, 27 Sikinos, 28 Sirna, 29 Siros, 30 Skiros, 31 Skopelos, 32 Thasos (= Thassos), 33 Tinos. Mean of %ENS (23.7) was used to group islands into two categories: islands with %ENS < 23.7 and islands with %ENS > 23.7.

The power function model is:

$$S = CA^z,$$

where S is the number of taxa considered (*i.e.*, END, SUB or ENS), A is the area and C and z are constants. The power function is approximated by the double log transformation:

$$\log S = \log C + z \log A.$$

The exponential model is:

$$S = \log C + z \log A.$$

The linear model is:

$$S = C + zA.$$

We performed regression analyses using both all islands (including those with $S = 0$), and only islands with $S > 0$. The inclusion of islands with $S = 0$ poses mathematical difficulties when the power function model is used, and various solutions have been proposed to avoid problems due to the logarithmic transformation (Williams, 1996). For simplicity, when islands with $S = 0$ were included in the power function model, we used the modified logarithmic transformation $\log(S+1)$ instead of more elaborate models, while $\log S$ was used when islands with $S = 0$ were omitted.

As to %END, %SUB and %ENS, regression analyses were performed both with A and with $\log A$. To study relations between number of taxa and distance to mainland (Dm), regression analyses were conducted between Dm and END, SUB, ENS, %END, %SUB and %ENS.

For correlations, a significant probability level was set up at $p < 0.05$.

RESULTS

Endemics (37 species and subspecies) and subendemics (23 species and subspecies) accounted for a large proportion of the Aegean tenebrionids (22% and 14% respectively). Some genera showed a very high cladogenesis in the study area. For example, the genus *Dendarus*, which has an important speciation center in the Aegean Area (Trichas et al., 1999), was represented on the studied islands by 10 species including 21 subspecies, and the genus *Dailognatha* by 4 species including 13 subspecies. However, only Kriti showed a high number of endemic taxa (22 taxa, 31%) and only few subendemic taxa (7 taxa, less than 10%); also, most of the subendemic taxa of Kriti occur only on circumcretean little islands.

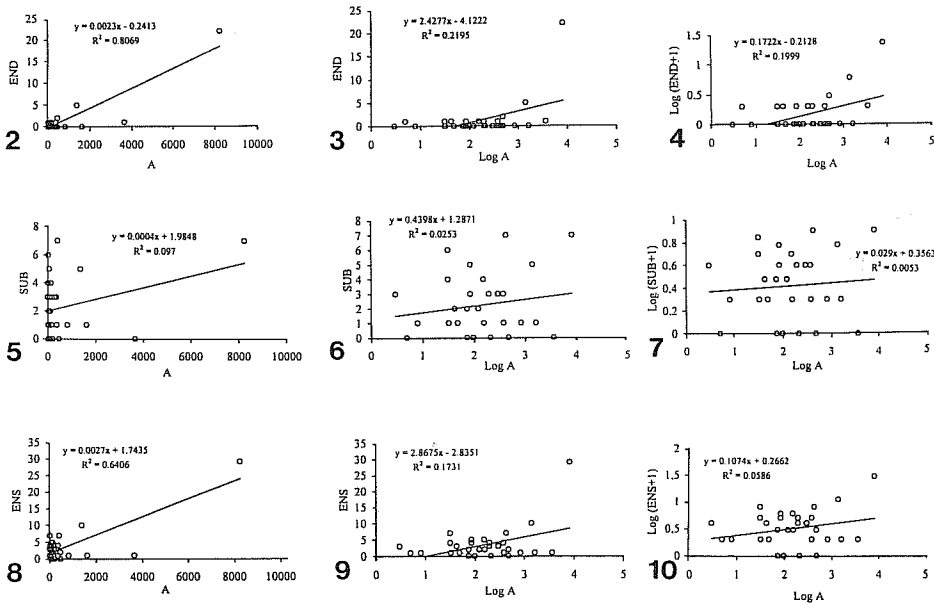
The remaining islands showed generally many subendemic taxa, but only few endemic taxa (Tab. I).

The mean value of %ENS was 23.72 ± 17.58 ($n = 33$). Interestingly, islands near the continental coasts showed %ENS lower than 23.72, while remote islands showed %ENS generally higher than 23.72 (Fig. 1).

Results of regression analyses are reported in Figs 2- 43. Using the linear function with all islands, a positive correlation was found between END and A (Fig. 2). When islands without endemics were removed from the analysis the correlation coefficient increased (Fig. 11). Using the exponential model, END was positively correlated with A (Fig. 3), but with a lower correlation coefficient. Likewise, correlation increased when islands without endemics were removed (Fig. 12). Using the power function model, a positive correlation coefficient was found with A (Fig. 4), increasing when islands without endemics were omitted (Fig. 13). %END was positively correlated with A when all islands were included (Fig. 20), and the correlation coefficient increased when islands without endemics were removed (Fig. 21). As to SUB, using all islands a positive correlation was found with Dm (Fig. 34). When islands without subendemics were removed, SUB was positively linearly correlated with A (Fig. 14), while correlation with Dm disappeared (Fig. 40). %SUB was positively correlated with Dm , both when all islands were included (Fig. 35) and when islands without subendemics were omitted (Fig. 41). A negative correlation was found between %SUB and $\log A$ using all islands (Fig. 23), and the correlation coefficient increased when islands without subendemics were omitted (Fig. 24). Using the linear model for all islands, ENS was correlated with A (Fig. 8). Correlation coefficient between ENS and A decreased using the exponential model (Fig. 9) becoming not significant when the power function model was used (Fig. 10). Likewise, when islands without endemics and/or subendemics were omitted, correlation was found between ENS and A by using the linear function model (Fig. 17) and the exponential function model (Fig. 18). Using all islands, %ENS was positively correlated with Dm (Fig. 37), and this correlation slightly increased when islands without endemics and/or subendemics were removed (Fig. 43). %ENS was negatively correlated with $\log A$ when all islands were included (Fig. 25), while this correlation disappeared when islands without endemics and/or subendemics were omitted (Fig. 31).

DISCUSSION

It is not surprising that END, SUB (when islands without subendemic taxa were omitted), and ENS increased with A , because the number of species (or, more generally, of taxa) in insular biota generally increases as A .



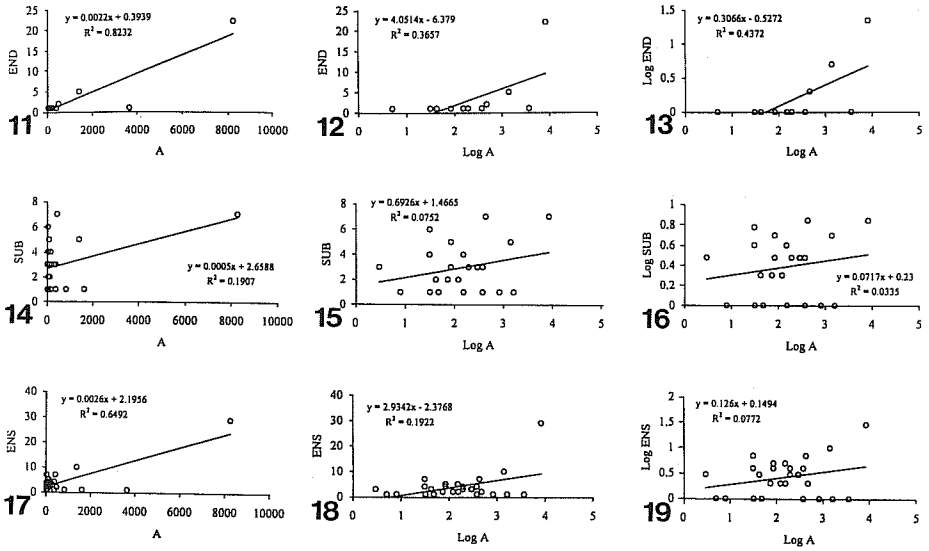
Figs 2-10 - Relation between number of endemic and subendemic taxa (species and subspecies) and island area by linear, exponential and power function models. END = number of endemic species and subspecies; SUB = number of subendemic species and subspecies; ENS = number of endemic and subendemic species and subspecies. All islands included.

In fact, area is an important determinant of tenebrionid taxonomic richness (number of species and subspecies) on the study islands (Fattorini et al., 1998), and a positive correlation between area and number of tenebrionid species and subspecies has been shown by Dajoz (1976) for various Greek Islands (including those used in this study but with slightly different estimations of taxonomic richness). The general relationship between area and total number of tenebrionid species and subspecies lies, however, outside the aim of this paper.

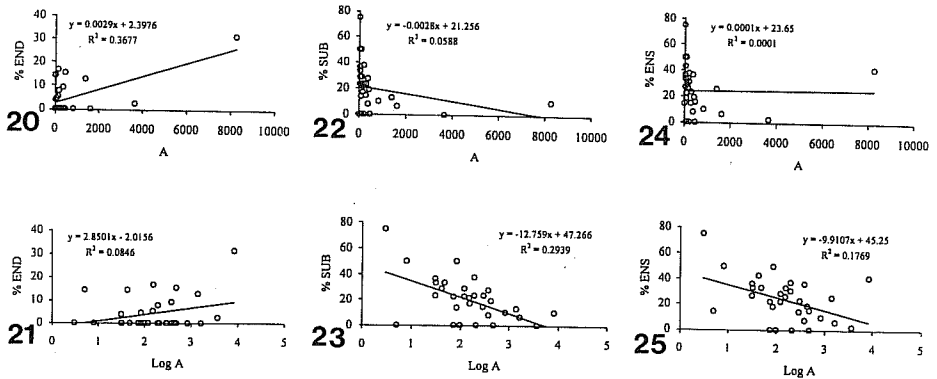
Island isolation represents an apparently important determinant of level of endemism. The obvious explanation of this fact is that increases in geographical distance from source pools make easy genetic isolation, resulting in higher levels of endemism. Indeed, remote islands showed high levels of endemism, while islands near the continental coasts evolved no or few endemic or subendemic taxa.

By contrast, the total number of tenebrionid species and subspecies seems to be not affected by *Dm*, suggesting a non-equilibrium model of relaxation following saturation involving palaeogeographical scenarios (Fattorini et al., 1998).

Palaeogeographical factors are probably involved also in the levels of endemism, accounting for the distribution of subendemic taxa and lack of correlation between %END and *Dm*.

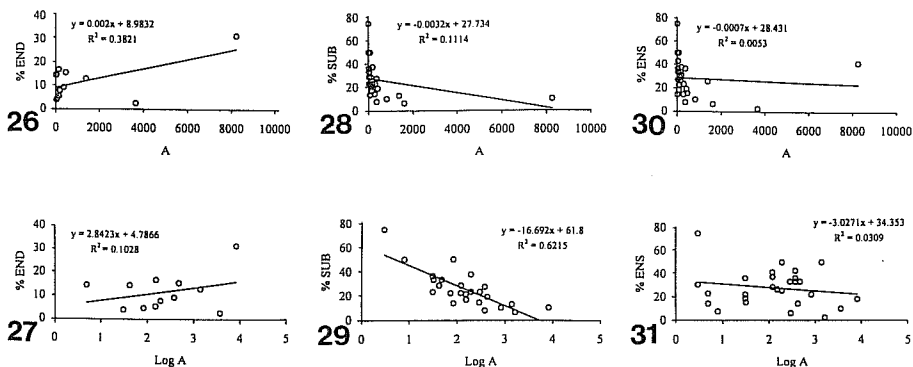


Figs 11-19 - Relation between number of endemic and subendemic taxa (species and subspecies) and island area by linear, exponential and power function models. END = number of endemic species and subspecies (islands without endemic omitted); SUB = number of subendemic species and subspecies (islands without subendemics omitted); ENS = number of endemic and subendemic species and subspecies (islands without endemics and/or subendemics omitted).



Figs 20-25 - Relation between percent number of endemic and subendemic taxa (species and subspecies) and island area. %END = percent number of endemic species and subspecies; %SUB = percent number of subendemic species and subspecies; %ENS = percent number of endemic and subendemic species and subspecies. All islands included.

The lowering of sea level in the Pleistocene made dry land out of extensive areas of shallow sea. Thus, the distances between the islands near the mainlands and the continental coasts were strongly reduced or disappeared, while only remote islands remained isolated from the mainlands (*e.g.*, Strid, 1970; Dermitzakis, 1990). However, most of the remote islands were mutually

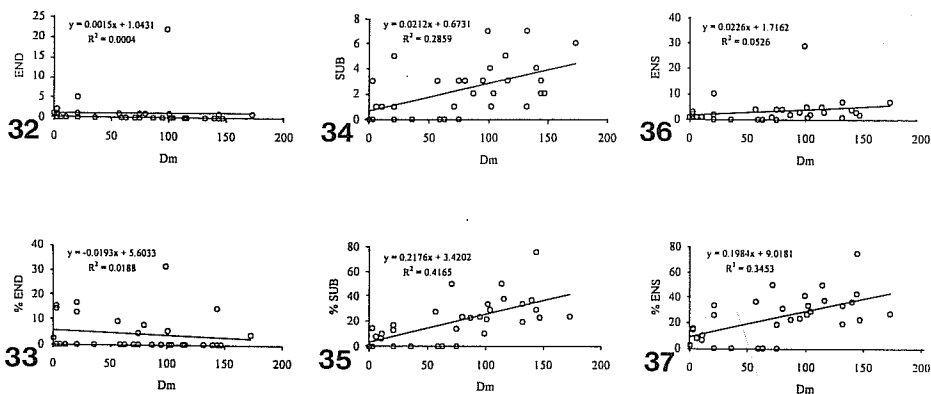


Figs 26-31 - Relation between percent number of endemic and subendemic taxa (species and subspecies) and island area. %END = percent number of endemic species and subspecies (islands without endemics omitted); %SUB = percent number of subendemic species and subspecies (islands without subendemics omitted); %ENS = percent number of endemic and subendemic species and subspecies (islands without endemics and/or subendemics omitted).

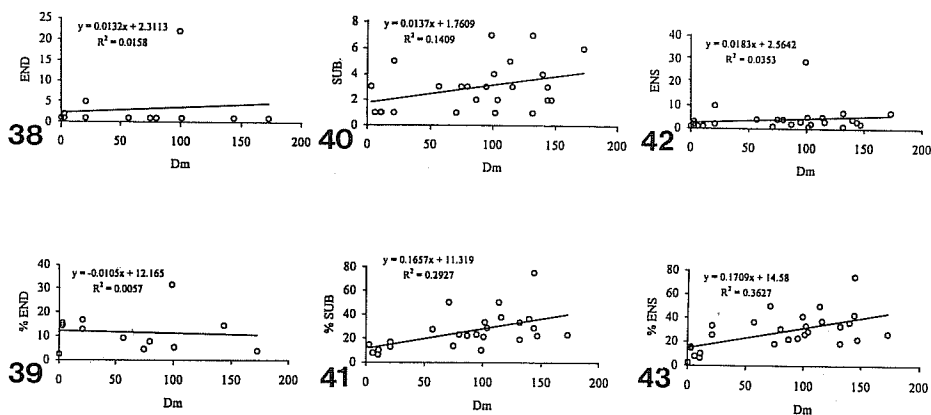
connected forming various Pleistocene island groups. As the islands forming a given island group were separated from those of other groups, they could have developed subendemic populations, *i.e.*, taxa occurring on islands of the same group but not on islands of other groups. Because the various island groups were presumably located at different distance to the mainland, the island groups with higher distance to mainland areas were probably subjected to higher faunal isolation, accounting for the positive relation between %SUB and *Dm*. On the other hand, only few islands were completely isolated, and, as revealed by palaeogeographical studies, this isolation was probably not related with the distance to the mainland. As an endemic taxon is a taxon occurring on only one island, endemics evolved generally only on these completely isolated islands; thus, their evolution was probably not affected by island distance to the mainland areas, as shown by the absence of correlation between %END and *Dm*. As ENS includes END, %ENS was less strongly correlated to *Dm* than %SUB.

The high number of tenebrionids endemic to Kriti can be related to the fact that this island was not connected with the mainland since Miocene (cf. Dermitzakis, 1990). Also at present, Kriti is geographically rather separated from other Aegean Islands. In spite of its location near the Anatolian coast, Rhodos shows a high level of endemism, but this fact is consistent with the geological history of the island. Rhodos, which is separated from the Anatolian coast by a strait that is over 300 m deep, remained separated from the mainland also in the Pleistocene and it was never connected with other islands except Karpathos (Dermitzakis, 1990).

By contrast, the Cyclades, which were mutually connected in various groups during Pleistocene sea level changes and which were probably disconnected about



Figs 32-37 - Relation between number of endemic and subendemic taxa (species and subspecies) and distance to closest mainland area. END = number of endemic species and subspecies; SUB = number of subendemic species and subspecies; ENS = number of endemic and subendemic species and subspecies; %END = percent number of endemic species and subspecies; %SUB = percent number of subendemic species and subspecies; %ENS = percent number of endemic and subendemic species and subspecies. All islands included.



Figs 38-43 - Relation between number of endemic and subendemic taxa (species and subspecies) and distance to closest mainland area. END = number of endemic species and subspecies (islands without endemics omitted); SUB = number of subendemic species and subspecies (islands without subendemics omitted); ENS = number of endemic and subendemic species and subspecies (islands without endemics and/or subendemics omitted); %END = percent number of endemic species and subspecies (islands without endemics omitted); %SUB = percent number of subendemic species and subspecies (islands without subendemics omitted); %ENS = percent number of endemic and subendemic species and subspecies (islands without endemics and/or subendemics omitted).

150,000 years ago (Beutler, 1979), have generally many subendemic taxa with only few endemic taxa.

Finally, the islands near the coasts show generally low levels of endemism, in accordance with both their Pleistocene connections with the mainland areas (Strid, 1970; Dermitzakis, 1990) and their present low *Dm*, which makes easy faunal immigrations.

A positive correlation was found between %END and A , but with a low correlation coefficient. Also, in contrast to Mac Arthur and Wilson's (1967: 173-175) theory, no correlations were found between %END and $\log A$. Interestingly, a negative high correlation was found between %SUB and $\log A$. Likewise, %ENS was negatively related with $\log A$, but with a lower correlation coefficient due to the positive endemic contribution.

This fact, in accordance with a relict model (Fattorini et al., 1998), suggests that random genetic drift, in turn related to a founder effect, could have substantially affected the evolution of subendemic taxa in the Aegean tenebrionids in past times.

In conclusion, present levels of endemism can be due to evolutionary processes related to palaeogeographical configurations of the Aegean area. Most probably, Pleistocene land-bridge connections between the mainland and the coastal islands precluded substantial genetic isolations; also, present presumably high rates of immigration allow a good genetic flow between island and mainland populations. As to the remote islands, during Pleistocene regressions many islands were mutually connected, forming various groups of islands. However, these groups can be considered isolated themselves, and new taxa may have evolved within each group. As the sea level was restored, each island group was newly divided into several islands; consequently, those taxa that evolved as endemic to an island group (*i.e.*, when the islands were connected) became subendemic to islands presently separated.

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