A biogeographical analysis of the tenebrionid beetles (Coleoptera, Tenebrionidae) of the island of Thasos in the context of the Aegean Islands (Greece)

SIMONE FATTORINI¹ & ADRIAN P. FOWLES²

¹Dipartimento di Biologia Animale e dell’Uomo (Zoologia), Università di Roma “La Sapienza”, Rome, Italy, and ²Countryside Council for Wales, Plas Penrhos, Bangor, UK

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Abstract
This research aimed to study the origin and the biogeographical relationships of the tenebrionid beetle (Coleoptera, Tenebrionidae) fauna of the island of Thasos, with reference to the other Aegean Islands. A total of 32 Aegean Islands and 170 taxa (species and subspecies), 23 of which occur on Thasos, were included in this study. Nine tenebrionid species are here reported for the first time from Thasos, including the first records of Platydema europaeum and Nalassus plebejus from the Aegean Islands. Several models (linear, exponential, power, logistic, Gompertz, Weibull and Lomolino functions) were used to test the species–area relationship. The power function appeared to be the most appropriate model and the parameters of the curve suggest a possible relict character for this fauna. The proportion of Balkan taxa on the islands sharply decreases from west to east, whereas the Anatolian taxa follow an opposite trend. Multi-dimensional scaling, Parsimony Analysis of Endemicity and discriminant function analysis revealed a clear faunal discontinuity between the western and central Aegean Islands on one side, and the islands close to the Anatolian coast on the other. This discontinuity, consistent with the persistence (from Messinian to Pleistocene) of a sea barrier between these two groups of islands, strongly supports the importance of Pleistocene island configurations in determining present distributional patterns. The comparative richness of the tenebrionid fauna on Thasos is enhanced by the proximity of the island to the mainland and the diversity of its surviving habitats.

Keywords: Distributional patterns, East Mediterranean, faunal similarity, island biogeography, species–area relationship, Tenebrionidae

Introduction
The zoogeography of the Aegean Islands has been long studied in order to highlight the major ecological and historical factors that are potentially responsible for the species–area relationships and present-day distributional patterns (e.g. Beutler 1979; Legakis and Kypriotakis 1994; Sfenthourakis 1999a, 1999b; Foufopoulos and Ives 1999; Sfenthourakis et al. 1999, 2004; Welter-Schultes and Williams 1999; Dennis et al. 2000, 2001; Sfenthourakis and Legakis 2001). The biogeography of the tenebrionid beetles of the...
Aegean has been studied by Dajoz (1987), Chatzimanolis et al. (2003) and thoroughly by Fattorini et al. (1999, 2000), Fattorini (2002a, 2002b) and Leo and Fattorini (2002), in a series of analyses focusing on levels of endemism, species distribution, and species–area relationship.

Recently, the influence of palaeogeography on the composition of the tenebrionid fauna of the Aegean Islands has been independently studied with different approaches in two nearly simultaneous papers: Hausdorf and Henning (2005) used partial Mantel tests and path analyses to study the influence of present geography, palaeogeography, and climate on the distribution on the central Aegean Islands, while Fattorini (forthcoming) used pairwise correlations, multiple regressions and path analysis to study the influence of present eco-geographic variables (including several measures of island geography and habitat diversity) on gamma diversity (species numbers), Canonical Correspondence Analysis for the influence of present and past island characteristics (represented by multi-dimensional spaces) on beta diversity (calculated as biogeographic similarity among islands), and fuzzy analysis to find island groupings based on beta diversity. The tenebrionid beetle fauna of the Aegean Islands has been investigated by naturalists for more than a century (cf. Fattorini et al. 1999). Most of the early records were summarized by Koch (1948), who described a number of new species and provided a wealth of new faunistic data. Following Koch, Schuster reported many records of Aegean tenebrionids between 1915 and 1936 (see Kühnelt 1965 for Schuster’s references). However, the most important faunal work concerning the distribution of tenebrionids in the Aegean area after Koch’s paper is Kühnelt’s (1965) catalogue of Greek Tenebrionidae. More recently, new information concerning the tenebrionids of the Aegean Islands has been published by Ardoin (1976), Dajoz (1976, 1983), Grimm (1981), Liebeggott (1982), Picka (1984), Legakis (1990), Whitehead (1997, 1999), Scupola (1998), Fattorini et al. (1999), Grimm and Schawaller (2000), Scupola and Lo Cascio (2001), Soldati and Soldati (2001), Leo and Fattorini (2002), Chatzimanolis et al. (2002) and Schawaller and Kakiopoulous (2002).

In spite of this long history of recording, not all the Aegean Islands have been equally investigated and data on the tenebrionids of Thasos are very scarce. The only published records are those included by Karnozickij (1959) and Ardoin (1976), with two other papers dealing with Xanthomus graecus by Whitehead (1999) and Ferrer and Whitehead (2002). This is a great pity because Thasos appears to be of crucial importance to correctly understand the biogeography of the Aegean area.

The Aegean Islands are located in the East Mediterranean, between the Greek mainland and the Anatolian coasts. The Balkans and the Anatolian peninsula seem to harbour very different faunas, thus representing clearly distinct regions (e.g. Oosterbroek and Arntzen 1992; Oosterbroek 1994; Lumaret and Lobo 1996; Sfenthourakis 1996a; Cook 1997; Sindaco et al. 2000). Due to their present location between these two different mainland areas, the Aegean Islands are expected to show transitional faunas and a transitional character for this fauna has already been demonstrated for the tenebrionid beetles by Fattorini (2002a). As a result of past colonization by land-bridge immigration and/or present-day over-sea dispersal, the proportion of Balkan tenebrionids (i.e. species that reached the Aegean Islands from the Balkan mainland) declines from West to East, while an opposite pattern can be observed for the Anatolian elements (i.e. species that reached the Aegean Islands from the Anatolian peninsula). However, in accordance with the persistence (from Messinian to Pleistocene) of a deep-sea barrier between the western and the eastern islands, these two groups appear to harbour very distinct faunas. The position of
the island of Thasos, however, was equivocal, this island being associated with both some Balkan and some Anatolian Islands according to the type of analysis used. This result appears rather surprising because Thasos is closer to the Balkan than the Anatolian coasts. Recent collections of tenebrionid material from Thasos permit re-analysis of the faunal relationships with the other islands in order to elucidate the biogeography of the Aegean.

The aims of this work are: (1) to update the present knowledge of the tenebrionid fauna of Thasos by new relevant records; (2) to discuss its zoogeographic composition; and (3) to revise the biogeographic position of this island in the framework of a more general discussion of the biogeography of the Aegean area.

Materials and methods

Study area

The Aegean Islands are located in the East Mediterranean, between the Greek and Turkish coasts (Figure 1). They are mainly aligned in a NW–SE direction and embrace various large islands (like 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 dominated by oak (*Quercus coccifera*), which was most probably the climax vegetation type of the Aegean area (Polunin and Walters 1985), and pine (*Pinus halepensis* and *P. nigra*). Habitat changes wrought by human activities, especially deforestation, are a key feature of the ecology of many 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. At present, all forests are seriously affected by human activities, grazing and summer fires being the main threat. On some islands, human activities may have caused the extinction of a few tenebrionid species associated with forest habitats. However, xylophilous species represent a minor component of the tenebrionid fauna considered here (about 20 out of a total of 138 species). Therefore, as for other animal groups such as terrestrial isopods and land snails (Sfenthourakis 1996a; Welter-Schultes and Williams 1999), the low number of species that may be absent from some islands as a result of extinction due to human activities is not expected to have any substantial influence on the general biogeographical patterns, but can play an important role in determining the observed species number on certain islands.

Thasos is approximately 6 km off the mainland Greek coast of Macedonia and has an area of approximately 328 km². Most of the island is mountainous, rising to 1203 m a.s.l., and lowland habitats are confined to a narrow coastal fringe. Olive production is a major industry and olive groves cover about one-fifth of the island. Elsewhere in the lowlands there are remnant dune systems (under increasing tourist pressure), a few highly threatened wetland ecosystems, and abundant *Cistus phrygana*. Maquis is more restricted as a result of grazing pressure and other broad-leaved woodland habitat types are very localized on Thasos. Oak woodland is rare but in a few localities there are relict Oriental plane *Platanus orientalis* and sweet chestnut *Castanea sativa* woods with abundant over-mature trees. The central zone is dominated by commercially forested Calabrian pine *P. halepensis* spp. *brutia*, extending up to ca 450 m a.s.l., and above this level black pine *P. nigra* ssp. *pallasiana* forests blanket most of the montane landscape.
Data sources

To study the possible relationship between Thasos and the other Aegean Islands, a total of 32 islands were included in this study (Figure 1; Table I). All of these islands are faunistically well known as a result of intensive surveys from the beginning of the past century to the present (cf. Fattorini et al. 1999; Fattorini 2000b, 2002a, 2002b).

On the Aegean Islands, several tenebrionid species are represented by different subspecies endemic to individual islands or groups of islands. All islands apart from Kriti have no more than one subspecies of a given species. In contrast, Kriti, the largest Aegean island, harbours several subspecies of some species. It is difficult, at present, to confirm the actual taxonomic status of these Cretan populations but as they occupy different areas on Kriti, and, probably, different habitats, they should be subject to the same biogeographic determinants as species in 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 we have counted these populations as different taxa. Species and subspecies number ($S$) was used in all analyses, the term “species” will be used in reference to tenebrionid overall richness for simplicity.

Data concerning species distribution among islands are the same as in Fattorini (2002a), updated as follows. The systematic treatment of the genus *Dendarus* and its distribution on islands were updated following Chatzimanolis et al. (2002, 2003), resulting in the suppression of *D. graecus montanus* from Kriti (a subspecies considered no longer valid) and in various nomenclatorial changes. Taxonomy and faunistics of the genus *Asida* was updated following Soldati and Soldati (2001), who reported *A. fairmairei graeca* from Andros. The occurrence on Rhodes of *Strongylium saracenum* (Schawaller and Kakiopoulos 2002) and *X. cyprius* (Ferrer and Whitehead 2002) was also noted.

Table I. Composition of the tenebrionid beetle fauna and geographical parameters from each of the 32 evaluated Aegean Islands.

| Island | $S$ | END | SUB | WID | ANA | BAL | La | Lo | A | Dm |
|--------|-----|-----|-----|-----|-----|-----|----|----|----|----|
| Amorgos | 7   | 0   | 2   | 3   | 0   | 2   | 36.5 | 25.59 | 121.1 | 104 |
| Anafi | 12  | 0   | 3   | 7   | 0   | 2   | 36.21 | 25.5 | 38.4 | 140 |
| Andros | 13  | 1   | 2   | 7   | 1   | 2   | 37.45 | 24.42 | 380 | 57 |
| Castelorizo | 8   | 1   | 0   | 4   | 3   | 0   | 36.08 | 29.34 | 7.3 | 2 |
| Chios | 10  | 0   | 0   | 6   | 3   | 1   | 38.22 | 26 | 842 | 11 |
| Euboea | 42  | 1   | 0   | 25  | 1   | 14  | 38.34 | 23.5 | 3658 | 0.3 |
| Folegandros | 7   | 0   | 2   | 3   | 0   | 2   | 36.37 | 24.54 | 32.1 | 132 |
| Ios | 9   | 0   | 1   | 5   | 0   | 3   | 36.42 | 25.24 | 107.8 | 147 |
| Karpathos | 15  | 0   | 3   | 8   | 3   | 0   | 35.4 | 27.1 | 301 | 93 |
| Kea | 6   | 1   | 0   | 4   | 0   | 1   | 37.34 | 24.22 | 130.6 | 20.5 |
| Kimolos | 3   | 0   | 1   | 1   | 0   | 1   | 36.48 | 24.34 | 35.7 | 102 |
| Kithnos | 4   | 0   | 0   | 3   | 0   | 1   | 37.25 | 24.28 | 99.3 | 36 |
| Kos | 26  | 0   | 4   | 17  | 5   | 0   | 36.5 | 27.1 | 290.3 | 3.5 |
| Kriti | 71  | 20  | 7   | 33  | 5   | 6   | 35.29 | 24.42 | 8260 | 99 |
| Lemnos | 10  | 0   | 0   | 9   | 0   | 1   | 39.54 | 25.21 | 460 | 59 |
| Lesvos | 17  | 0   | 1   | 13  | 2   | 1   | 39.1 | 26.2 | 1630 | 10.5 |
| Mikonos | 10  | 0   | 4   | 3   | 0   | 3   | 37.29 | 25.25 | 85.5 | 114 |
| Milos | 19  | 1   | 3   | 10  | 1   | 4   | 36.41 | 24.15 | 150.6 | 100 |
| Naxos | 36  | 0   | 5   | 23  | 2   | 6   | 37.02 | 25.35 | 428 | 130 |
| Pano Koufonissi | 12  | 0   | 4   | 6   | 0   | 2   | 36.56 | 25.59 | 3.8 | 147 |
| Paros | 8   | 0   | 2   | 4   | 0   | 2   | 37.08 | 25.12 | 194.5 | 116 |
| Rhodes | 43  | 4   | 5   | 24  | 9   | 1   | 36.1 | 28 | 1400 | 21 |
| Samos | 14  | 1   | 0   | 7   | 6   | 0   | 37.48 | 26.44 | 476.2 | 2.8 |
| Santorini | 26  | 1   | 5   | 17  | 1   | 2   | 36.24 | 25.29 | 31 | 173 |
| Serifos | 8   | 0   | 0   | 6   | 0   | 2   | 37.11 | 24.31 | 73.2 | 64 |
| Sifnos | 9   | 0   | 2   | 3   | 1   | 3   | 36.59 | 24.4 | 73.2 | 87 |
| Sikinos | 8   | 0   | 2   | 3   | 1   | 2   | 36.39 | 25.06 | 41 | 144 |
| Siros | 23  | 1   | 2   | 17  | 1   | 2   | 37.26 | 24.54 | 83.6 | 75 |
| Skiros | 11  | 0   | 0   | 6   | 0   | 5   | 38.53 | 24.32 | 209 | 75 |
| Skopelos | 7   | 0   | 0   | 1   | 0   | 6   | 39.1 | 23.4 | 96 | 21 |
| Thasos | 23  | 0   | 0   | 18  | 1   | 4   | 40.41 | 24.47 | 379 | 6 |
| Tinos | 13  | 1   | 2   | 6   | 1   | 3   | 37.38 | 25.1 | 194.3 | 80 |

*S*, tenebrionid richness (number of species and subspecies); $END$, number of endemic taxa; $SUB$, number of sub-endemic taxa (i.e. taxa occurring on more than one island but that are endemic to the Aegean archipelago as a whole); $WID$, number of widespread taxa; $ANA$, number of Anatolian taxa; $BAL$, number of Balkan taxa; $La$, latitude ($^\circ\ N$); $Lo$, longitude ($^\circ\ E$); $A$, area ($\text{km}^2$); $Dm$, distance to the nearest mainland ($\text{km}$).
Gonocephalum affine and G. setulosum from Kriti (Ferrer 1995) were added. Faunal records for Thasos were updated according to new data reported below. As a whole, 170 taxa (138 species and 32 subspecies) were ascertained to occur as native populations on the study islands.

Stenosis sp. from Karpathos and Neatus picipes from Euboea (cf. Fattorini et al. 1999), were omitted from analyses dealing with distribution patterns due to the lack of detailed information, but they were counted in analyses dealing with total species numbers. We have omitted from the analysis some species cited by various authors from the study islands because of their synanthropic (and hence probably introduced), transient, exotic or uncertain distribution. We have also omitted the whole subfamily Alleculinae, and, among the subfamily Lagriinae, the tribe Lagriini. Since Watt (1974) these two taxa, formerly regarded as distinct families, are currently considered as subfamilies of Tenebrionidae by many authors (cf. Doyen and Tschinkel 1982). However, at least for the Palaearctic fauna, they are ecologically quite different from most of the other Tenebrionidae and we have omitted these groups because of their very high dispersal ability and their very poorly known distribution within the study area. A detailed account of the criteria used to reject data can be found in Fattorini et al. (1999). Even if some islands are better known than others (Kriti and some of the Cyclades are the best studied), 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 be not substantial.

For Thasos we included both previous (literature) and new records to construct a checklist (Table II) for the island. The following records, reported by Karnozickij (1959), were omitted because they were clearly wrong. Records of *Cephalostenus elegans* are to be referred to *C. orbicollis*. *Dendarus emarginatus* is probably synonymous with *D. lugens*, which is absent in the Aegean area, and all records from Thasos are to be referred to *D. messenius*, a quite similar species (Fattorini et al. 1999). The occurrence on Thasos of *Helops coeruleus* is unlikely; most probably the species was confused with *H. rossii*, which has recently been collected on Thasos.

We were able to examine, and confirm, most of the material cited by Ardoin (1976), now preserved at the Zoological Museum of “La Sapienza” University, Rome. The following records of specimens collected by A.P.F. between 1993 and 2003 represent nine species newly reported from Thasos: *Ammobius rufus*, Skala Potamia, sand dunes, 22 May 1999; *Bolitophagus reticulatus*, Skala Potamia, under bark of dead poplar, 29 September 2001; *Diaclina fagi*, Skala Potamia, under bark of dead poplar, 29 September 2001; *Dichillus carinatus*, Limenas Upper Valley, maquis, 19 September 1995; *G. granulatum nigrum*, Cap Prinos, sandy coastal grassland, 15 September 1995; Limenas, Aberdeen Studios, olive groves, 7 May 1997; *Helops rossii*, Panagia Valley, sweet chestnut forest, 22 May 1999; *Nalassus plebejus*, Limenas Valley, beaten off poplars, 6 May 2003; *Opatrum obesum*, Skala Sotira, shingle beach, 16 September 1995; Cap Prinos, sandy coastal grassland 15 September 1995; *Platydema europaeum*, Limenas, Vera Lili, olive groves, 16 September 1993; Cap Prinos sandy coastal grassland, 15 September 1995; Panagia Valley, under sweet chestnut bark, 16 September 1995.

Species–area relationship in the Aegean Islands

To study the relation between species and area, several different mathematical models have been proposed in recent decades. According to Tjørve (2003), species–area curves can be
classified into two main categories: convex curve models and sigmoid models. Based on Tjørve’s (2003) revision, we selected the following three convex models: the exponential function, the power function, and the negative exponential.

The power function model is:

$$S = CA^z,$$  \hspace{1cm} (1)

where \(S\) is the number of species, \(A\) is the area, and \(C\) and \(z\) are constants.

The power function is approximated by the double log-transformation:

$$\log S = \log C + z \log A.$$  \hspace{1cm} (2)

The exponential model is:

$$S = \log C + z \log A.$$  \hspace{1cm} (3)
The negative exponential model is:

\[ S = b_0(1 - \exp(-b_1A)). \]  

Many empirical studies that appear to fit the power function model (in its linear form) have led to its almost routine use in studies of island biogeography. However, there is no \textit{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 and McCoy 1979; Fattorini 2002b). The power function model poses some statistical and biological problems. Equations 1 and 2 are not statistically equivalent for least-square regression, because different quantities are minimized (Wright 1981). If the error term is multiplicative, the logarithmic transformation is correct. If the error term is additive the logarithmic transformation is incorrect, and a non-linear least-squares regression should be applied. According to Wright (1981), the error in \( S \) is probably independent of \( A \), and a non-linear least-squares fit is appropriate. However, Fattorini (2002a, 2002b) suggested that the error in \( S \) can be dependent of \( A \). It is reasonable to suppose that our estimations of faunal richness are more accurate for small islands, which have fewer species, than for large islands, which are more difficult to survey completely. Thus, our estimate of \( S \) is associated with area and the logarithmic transformation may be appropriate. In addition, in non-linear regression, the parameter estimates are too heavily influenced by large values, causing shortcomings in the use of this technique (Welter-Schultes and Williams 1999). However, for comparison purposes, we used both Equations 1 and 2 in the present study.

Recently, Lomolino repeatedly (2001, 2002) proposed that the species–area relationship should be of sigmoidal shape. If an asymptotic shape is required, sigmoid models should be selected as the most direct way to fit data.

Based on Tjørve’s (2003) revision, we selected the following four models: logistic function:

\[ S = b_0/(1 + \exp(-b_1A + b_2)), \]  

Gompertz model:

\[ S = b_0 \exp(-\exp(-b_1A + b_2)), \]  

cumulative Weibull distribution:

\[ S = b_0 \left( 1 - \exp\left( -b_1A^{b_2} \right) \right), \]  

cumulative Weibull distribution with location parameter:

\[ S = b_0 \left( 1 - \exp\left( -b_1(A - b_2)^{b_3} \right) \right), \]  

Lomolino’s function:

\[ S = b_0 \left/ \left( 1 + \left( b_1 \log(b_2/A) \right)^{b_3} \right) \right), \]  

where \( b_0, b_1, \) and \( b_2, \) are optimized parameters.

In a previous study, Fattorini (2002a, 2002b) also used a linear model:

\[ S = C + zA. \]
This model has been rarely applied and it is not treated by Tjørve (2003), but for comparative purposes this model has also been applied here.

The most commonly used statistics to compare different regressions is $R^2$. However, great care should be taken in using the $R^2$ goodness-of-fit statistic to compare different models. This statistic is problematic for comparing models based on different transformation of the $Y$-axis (Quinn and Keough 2002). The $R^2$ computed from log-transformed variables holds only for the linearized space obtained by the transformation and cannot be compared with the $R^2$ computed from the untransformed data. Kvaseth (1985) suggests computing an alternative $R^2$ called here $FI$ (fit index) according to the equation:

$$FI = 1 - (RSS/TSS),$$

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

In $TSS$ and $RSS$ calculations, $\hat{Y}_i$ is the backtransformed value of the estimated $Y$ in the transformed space and $\bar{Y}$ 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 $c = 2.65 \times S_{yx}^2$ and $S_{yx} = $ standard error of estimate in log10 units (Ferguson 1986).

The $FI$ of the linearized power function model can be compared to the $R^2$ of the linear and exponential model. Another regression statistic that can be used to compare models is the standard error of estimate. However, the standard errors obtained directly from the different models cannot be compared each to other, because they are derived by different transformations. Fattorini (2002a, 2002b) used an antilogarithmic backtransformation of the standard error of estimate of the linearized power function, but this procedure is statistically incorrect (cf. Krebs 1999).

To compare the standard error of estimate of different models, they have to be calculated directly in actual units. We calculated the standard error of estimate ($S_e$) in actual units according to the following formula (Parresol 1999):

$$S_e = \sqrt{(RSS/(n-p))},$$

where $p =$ number of model parameters (for proposed models $p = 2$).

Finally, we calculated also the coefficient of variation ($CV$), another possible measure of comparison suggested by Parresol (1999):

$$CV = (S_e/\bar{Y}) \times 100.$$  

There is no direct $R^2$ defined for non-linear regression. Thus, for the non-linear models, $R^2$ goodness-of-fit statistic was 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.

To compare both linear and non-linear models with different numbers of parameters, we used the adjusted coefficient of determination ($R_a^2$), as used by He and Legendre (1996).
for species–area model fitting. The coefficient is calculated as:

\[ R^2_a = 1 - \frac{(n-1)RSS}{(n-k)TSY}, \]

where \( n \) is the number of islands, \( k \) is the number of parameters in a model, and \( TSY \) is the sum of the squared \( Y \) values.

Models were also compared using the “root mean-square deviation” (\( \Delta \)), i.e. the square root of the RSS divided by the number of samples (cf. He and Legendre 1996).

Equations 1, 2, and 10 were applied using the standard method of least squares linear regression. Equations 3–9 were applied using the Quasi Newton estimation method (start values: 1 for all parameters; initial step size: 0.5 for all parameters). For the cumulative Weibull model, start values were set up at 0.0000001 to obtain a more valuable result. For the negative exponential model, valuable results were obtained changing start value of \( b_0 \) at 100.

In order to determine the “best fit”, all alternative models were also examined for lack of systematic error (Sugihara 1981) checking for homogeneity of variance and normality (Zar 1984). Specifically, we plotted the residuals against the independent terms and examined them for non-linearity and non-constancy of error variance. After visual inspection, the Pearson correlation coefficient was applied to test possible linear trends. The Shapiro–Wilk test was used to test for normality of error terms.

The estimated value of species richness obtained for Thasos by each model (after backtransformation according to the aforementioned rules for the linearized power model) was then compared with the actual one.

Analyses were performed using Statistica software version 4.5 (Statsoft Inc. 1993). In all tests a minimum probability level of \( P \leq 0.05 \) was accepted (all tests were two-tailed).

**Zoogeographical composition of Thasos tenebrionids**

As the proportion of the Balkan taxa on the Aegean Islands is expected to decline from west to east, and an opposite pattern is expected for the Anatolian taxa, regression analyses were used to study relationships between longitude and percentages of Balkan and Anatolian taxa. To normalize data, longitude was log10-transformed and proportions arcsin-transformed.

From an aerographic point of view, the tenebrionids of Thasos can be grouped in certain geographic categories including species that share similar geographic ranges. The procedure of aerographic classification consisted of mapping the geographical range of each species and conditional attribution of it to one of the types of geographical ranges. Two main approaches to aerographic classification can be distinguished. One approach is based on the concept of the centres of origin, widely criticized by vicariantist biogeographers, being founded on speculative and non-provable assumptions (Fattorini 2000a). Another approach is purely phenomenological and is based only on the contemporary similarity of the species ranges. As in many other studies (e.g. Sfenthourakis 1996a; Chikatunov et al. 1997; Krasnov and Shenbrot 1998) we referred to the latter approach. For this purpose, we used as types of geographical ranges the “chorotypes” proposed by Vigna Taglianti et al. (1999).

On the basis of their distribution within the study area, the tenebrionids of Thasos were arranged in the following distributional classes (Table II): (I) Balkan (i.e. taxa occurring in the Balkans and on the Aegean Islands, but not in the Anatolian peninsula); (II) Anatolian (i.e. taxa occurring in the Anatolian peninsula and on the Aegean Islands, but not in the...
Balkans); (III) Widespread (i.e. taxa occurring both in the Balkans and in the Anatolian peninsula, as well as on the Aegean Islands).

**Faunal similarity**

A matrix for binary data (absence=0; presence=1) was compiled for the taxa occurring on each island. This matrix is that published by Fattorini (2002a), updated as described in “Data sources”. In order to evaluate the similarities of the tenebrionid faunas found on the Aegean Islands, the data were studied via Q-mode, which measures the relationship among objects (islands) based on descriptors (taxa). A large number of coefficients that use binary data to measure association between objects is presently available (Shi 1993). A favourable characteristic of similarity coefficients for biogeographical purposes is their ability to exclude double-zeros, otherwise regions with low species richness would be grouped on the basis of shared absences rather than presences (Legendre and Legendre 1983). On the basis of Shi’s (1993) review, and availability in NTSYS software (Rohlf 1993), Dice’s, Jaccard’s, Kulczynski’s #2, and Ochiai’s coefficients were utilized in this research. Formulae are given in Legendre and Legendre (1983) and Rohlf (1993). An important difference among these coefficients is the effect of sample-size, as islands with few species will be more closely ranked where sample-size effect is highest. The effect of sample-size is strongest in Kulczynski’s #2, moderate in Ochiai’s, and low in the remaining two (Shi 1993).

All measures gave very similar outcomes. We selected Jaccard’s index because this is widely used in biogeographical analyses. The distance-matrix obtained with Jaccard’s index was then subject to a non-metric multi-dimensional scaling (MS) using Statistica software (version 4.5). This technique is designed to construct a “map” showing the relationships between a number of objects, given only a table of distance or similarity between them. Using MS all objects were compared together, while clustering methods find the closest relationships within pairs of objects. The goodness of results obtained by this method is measured as stress values. Stress is the term applied to variance between distance and similarity (Shi 1993). As stress provides an indication of distortion relative to the original data, small values of stress (close to 0) are desirable. We started by extracting two dimensions, obtaining a stress value of 0.227. Extracting a third dimension reduced the stress to 0.154. However, here we present the two-dimensional plot because a three-dimensional plot was much less clear.

To assess whether the island faunal composition actually reflects a biogeographical discontinuity between “Balkan” and “Anatolian” islands according to their geographical position, a Discriminant Function Analysis (DFA) was performed using Statistica software (version 4.5). Based on their geographical position, islands were classified a priori into two groups: the “Anatolian Islands” (i.e. Castellorizo, Chios, Kos, Lesvos, Samos, Lemnos, Rhodos, and Karpathos) and “Balkan Islands” (all others). Kriti was excluded due to its endemic distinctiveness and peculiar location. The islands were discriminated according to the proportion of species belonging to different distributional patterns. As the percentages of Balkan, Anatolian, widespread, sub-endemic and endemic taxa add to 100% for each of the 31 islands, this means that any one of the five percentage variables can be expressed as 100 minus the remaining variables. It was therefore necessary to omit at least one of the variables to calculate canonical discriminant functions. We omitted proportions of both endemic and widespread taxa because these classes were uninformative for assessing relationships.
Parsimony Analysis of Endemicity

Parsimony Analysis of Endemicity (PAE) was introduced by Rosen (cf. Rosen 1988) for examining presence/absence data of taxa by areas to define regions with shared presence of taxa. This differs from similarity analyses in that clustering is based on individual characters within areas rather than overall similarity between areas. PAE shows the relationship between geographical areas using a cladistic approach. The areas are treated as traditional taxa (areas-as-taxa) and the distributions of the taxa serve as the characters (taxa-as-characters). PAE groups areas by their shared taxa according to the most parsimonious cladogram(s). Any taxon occurring in more than one area helps to illuminate the relationship between the areas, hence, is an informative taxon-as-character. By contrast, taxa found in a single area are equivalent to autapomorphies, being uninformative for assessing relationships.

Brooks and van Veller (2003) questioned the utility of PAE in historical biogeography, showing that in most circumstances this technique is less able in recovering historical patterns than phylogenetically based methods. However, for the Aegean Islands, phylogenetical reconstructions are available only for the genus *Dendarus* of certain islands (Chatzimanolis et al. 2003), a very limited sub-sample of the entire tenebrionid fauna.

As no phylogenetically based method can be applied to our dataset, PAE remains the only applicable cladistic method. Also, many arguments may be reported in defence of PAE, showing that it furnishes valid reconstructions, especially for organisms which have limited dispersal abilities and speciate in a vicariant manner (Morrone and Escalante 2002), a state of affairs that appears quite realistic for the Aegean tenebrionids. According to Cracraft (1994), speciation by vicariance and biotic dispersion produces historically structured (hierarchical) species assemblages, while long-distance dispersal results in non-hierarchical species assemblages. To test whether PAE results are hierarchical or not they can be compared with geological information. Congruence between area cladograms and palaeogeographical reconstructions is evidence for vicariance and biotic dispersion, whereas incongruence is likely to reflect dispersal and/or ecological factors (cf. Rosen 1988; Glasby and Alvarez 1999). Thus, PAE can be considered a valid alternative to phenetic analysis (Morrone and Escalante 2002) when phylogenetic data are lacking.

Morrone and Escalante (2002) pointed out that, in defining geographical units, natural areas are preferable instead of quadrats. As islands are unambiguously defined natural areas, islands appear to be particularly suited for a PAE analysis.

In this study, each island represented an area-as-taxon, and each taxon a taxon-as-character. The number of informative taxa-as-characters was 76 out of 170. The cladistic analysis was performed using PAUP 4.0b8 (Swofford 1998). All taxa-as-characters were equally weighted. As in other studies using PAE (Vargas et al. 1998; Glasby and Alvarez 1999; Vega et al. 1999; Bisconti et al. 2001; Aguilar-Aguilar et al. 2003), characters were polarized using a hypothetical area with all zeroes as the outgroup.

Two distinct analyses were performed. In a first analysis, characters were coded as unordered (Wagner parsimony), as in previous PAE studies (e.g. Vargas et al. 1998; Garcia-Barros et al. 2002). For a second analysis, characters were coded as Dollo. Morrone and Escalante (2002) observed that in an area cladogram convergences would be impossible, because a taxon cannot appear separately in two areas not linked biogeographically and suggested using the ACCTRAN optimization, which favours reversals rather than convergences. However, the same authors recognized that it is impossible to distinguish *a priori* between primitive absences or real reversals (extinctions), so absence can only be coded “0” instead of either “0” or “?”, as it should be. Fattorini
(2002a) used PAE under Dollo parsimony. Using a Dollo parsimony, a taxon-as-character can appear only once, but can be lost as many times as necessary. In biogeographical terms, extinction is more likely than colonization. This procedure may be a valuable way to circumvent the problems of convergences. Such assumption is also consistent with the hypothesis of a relict fauna and with the sedentary character of most tenebrionids.

As a result of “all 0” polarization, areas having few taxa will tend to be viewed as being primitive. Also, as observed by Glasby and Alvarez (1999), absence may be the result of (1) taxon never occurred in sample area, (2) taxon became extinct, or (3) taxon not yet been discovered. Dollo parsimony should reduce such biases. Since according to the Dollo parsimony 1-0 is more likely than 0-1, absences due to incomplete knowledge are easily considered as homoplastic characters.

In both analyses, a heuristic research, involving firstly the calculation of an initial set of trees by random stepwise addition and then branch swapping with tree-bisection-reconnection, was performed. Default options were used (search on non-minimal trees (MULTREES) on; steepest descent off; zero-length branches collapsed) with 1000 replicates. The following statistics were calculated: consistency index (CI) excluding uninformative characters, homoplasy index (HI) excluding uninformative characters, retention index (RI) and rescaled consistency index (RC).

Results

Faunal account

Based on literature records and examined specimens, 23 species of native tenebrionid beetles occur on Thasos (Table II). Some species are particularly notable for their ecology and distribution. *Bolitophagus reticulatus* is a mycophagous species, associated with polypores living on trees, especially beech (Gridelli 1956), previously known from Greece only from the Peloponnese (Kühnelt 1965). *Diaclina fagi* is very rare in Greece, this record being the fourth known location. The ecology of this species is poorly known. In Greece, it was found beneath beech bark (Dajoz 1976) and among mould in a heap of old soil (Moragues 1989). Ponel and Moragues (1988) and Soldati and Soldati (1992) found it under the bark of dead poplar (as on Thasos) among mushroom hyphae, and Scupola (2000) under bark, beneath goose litter, within hay, and feeding on mould. *Platydema europaeum*, a mycetophagous species apparently linked to polypores on pine logs and trunks, was previously known from Greece only from the mainland (Mt. Taygetos) and Lesvos (Kühnelt 1965). *Helops rossii* and *Nalassus plebejus*, previously known for Greece from the mainland and the Ionian Islands (Kühnelt 1965), are recorded here for the first time from an Aegean Island.

Among the psammophilic species two are of particular interest: *Opatrum sabulosum* and *X. graecus*. *Opatrum sabulosum* is known from continental Greece (typical form; Dajoz 1983), where it appears to be very rare, Nissiros (Liebegott 1982) and Lesvos (where the population has been referred to the ssp. *lucifugum*, apparently occurring in various eastern European areas). *Xanthomus graecus* possesses a distribution restricted to the Peloponnese and Thasos island (Ferrer and Whitehead 2002).

The species may be grouped according to their main habitat preferences into the following guilds:

1. Stenotopic, strictly psammophilous, species, living on sandy dunes: *A. rufus*, *Catomus consentaneus*, *Tentyria rotundata angulata*, *X. graecus*.
2. Euryoecious geophilous and psammophilous species, associated with sandy dunes, Oleo-Ceratonion vegetation and maquis: Graecopachys quadricollis, O. obesum, O. sabulosum sabulosum, Pimelia subglobosa, Zophosis punctata punctata.

3. Geophilous species, associated with maquis and Quercus ilex vegetation (Dajoz 1987): Cephalostenus orbicollis, Dialognatha quadricollis carceli, D. messenius, D. moesiacus, G. granulatum nigrum.

4. Xylophilous, generally mesophilic species, associated with various trees: B. reticulatus, Diacлина fagi, N. plebejus (poplars), Helops rossii, Menephilus cylindricus cylindricus (oaks), P. europaeum (pines).

Species–area relationships

Species richness was significantly correlated with area of the Aegean Islands for all linear models (Table III). Based on $F_I$ and low standard error statistics, the linear model appears to be the best fit. Note that the power function, in its linear form, fitted better than the exponential one. However, both the linear and the exponential models gave residuals that strongly deviate from normality. Also, residuals of the exponential model showed a clear trend when plotted against the independent term. Thus, the power function model should be selected as the “best fit”, because of homogeneity of variance and normality of residuals, high $F_I$ and low standard error statistics.

As to the curvilinear models (Table IV), all of them gave residuals uncorrelated with the independent terms. However, both the Gompertz and the Logistic models appeared inadequate because of the non-normality of residuals.

Lomolino’s model gave a poor fit, compared with the other models, with three parameters. It should be also noted that the parameters estimated by Lomolino’s model are very unrealistic, because the expected maximum number of species ($b_0$; cf. Lomolino 2001) is tremendously high (about 2.5 times the entire European tenebrionid fauna, which is estimated to be 1780 species and subspecies by one of us (S.F.) for the FaunaEuropaea project: www.faunaeur.org). Setting the starting values at $b_0=71$ (tenebrionid species and subspecies occurring on Kriti, the island with the highest value) and $b_2=428$ (the area of Naxos, an island which harbours 36 species, about half of Kriti), did not improve the results ($b_0=3850.481$, $b_1=1.516$, $b_2=151,172 \times 10^3$). If $b_0$ is fixed to 170, the total species richness, no valuable results were obtained. Weibull four-parameters was the asymptotic model which gave the best estimate of total richness (about 243 species for the entire archipelago). Also, Lomolino’s model was similar to the power function, which has only two parameters. As observed by Lomolino himself (2001), it is not surprising that, in general, functions with three parameters give higher $R^2$ values than models with two parameters (as the power function). So, one could expect that Lomolino’s three-parameters function should be better than the power function. On the contrary, in the study area the two functions fitted the data equally well. Also, the other three-parameter equations did not explain a substantially higher variance than the power function. The power function explained the same amount of variance as the Weibull function, using only two parameters. As a whole, the Gompertz and the logistic models should be discarded because of the non-normality of residuals, while the Lomolino function appears to give unrealistic predictions. Both the power function and the Weibull distribution can be accepted as “best fit”, but the power function appears preferable because it is simpler. Also, the Weibull distribution (without location parameter) provides alternative solutions (with very similar
Table III. Linear models of species–area relationship.

| Model        | Equation                          | \(S_e\) | \(CV\) (%) | \(FI\) | \(R^2\) | \(PS\) | \(HR\) | \(NR\) | \(\Delta\) |
|--------------|-----------------------------------|---------|------------|-------|--------|--------|--------|--------|----------|
| Linear       | \(S = 11.750 + 0.0076A\)         | 8.153   | 49.220     | 0.685 | 0.864  | 14.623 | \(r=0.000, P=1.000\) | \(W=0.833, P<0.001\) | 7.894    |
| Exponential  | \(S = -12.663 + 13.191 \log A\) | 11.028  | 66.584     | 0.423 | 0.750  | 21.353 | \(r=0.505, P=0.003\) | \(W=0.922, P=0.027\) | 10.678   |
| Power        | \(\log S = 0.529 + 0.260 \log A\) | 9.839   | 59.950     | 0.541 | 0.801  | 18.677 | \(r=-0.237, P=0.191\) | \(W=0.967, P=0.483\) | 9.527    |

\(S_e\), standard error of estimate in actual units (for linear and exponential models it is simply the standard error of estimate); \(CV\), coefficient of variation; \(FI\), fit index (for linear and exponential models it is the \(R^2\)); \(R^2\), adjusted \(R^2\); \(PS\), predicted value of species richness on Thasos; \(HR\), homogeneity of variance (evaluated as Pearson correlation coefficient between residuals and independent term); \(NR\), normality of residuals (tested by Shapiro–Wilk test); \(\Delta\), root mean-square deviation. For all regressions, \(P<0.001\). *Corrected for bias in backtransformation.

Table IV. Curvilinear models of species–area relationship.

| Model                               | Equation                                      | \(R^2\) | \(R^2\) | \(PS\) | \(HR\) | \(NR\) | \(\Delta\) |
|-------------------------------------|-----------------------------------------------|---------|---------|--------|--------|--------|----------|
| Power                               | \(S = 1.547A^{0.412}\)                      | 0.660   | 0.853   | 17.901 | \(r=0.033, P=0.857\) | \(W=0.964, P=0.408\) | 8.198   |
| Logistic                            | \(S = 72.230/(1+\exp(-0.0006A+1.619))\)     | 0.683   | 0.858   | 14.396 | \(r=0.033, P=0.858\) | \(W=0.833, P<0.001\) | 7.921   |
| Negative exponential without location parameter | \(S = 53.952(1-\exp(-0.0085A))\)              | 0.420   | 0.749   | 14.396 | \(r=-0.011, P=0.951\) | \(W=0.957, P=0.264\) | 10.702  |
| Negative exponential with location parameter | \(S = 79.399(1-\exp(-0.0002(2A+719.642)))\) | 0.696   | 0.863   | 15.603 | \(r=0.071, P=0.698\) | \(W=0.9012, P<0.017\) | 7.755   |
| Gompertz                            | \(S = 76.620 \exp(-0.0004A+0.643)\)          | 0.691   | 0.861   | 14.587 | \(r=0.021, P=0.909\) | \(W=0.854, P<0.001\) | 7.821   |
| Lomolino                            | \(S = 4576.968/(1+(1.516 A^{0.326}(1+\exp\{\ln(2.32E+8)/A\}))\) | 0.659   | 0.848   | 17.896 | \(r=0.032, P=0.863\) | \(W=0.964, P=0.417\) | 8.206   |
| Weibull without location parameter  | \(S = 2088.136(1-\exp(-0.0007A^{0.415}))\)   | 0.659   | 0.847   | 17.912 | \(r=0.039, P=0.833\) | \(W=0.964, P=0.410\) | 8.206   |
| Weibull with location parameter     | \(S = 243.293(1-\exp(-0.0009(A+344.133)^{0.651}))\) | 0.703   | 0.862   | 15.716 | \(r=0.0083, P=0.964\) | \(W=0.896, P<0.005\) | 7.661   |

\(R^2\), adjusted \(R^2\); \(PS\), predicted value of species richness on Thasos; \(HR\), homogeneity of variance (evaluated as Pearson correlation coefficient between residuals and independent term); \(NR\), normality of residuals (tested by Shapiro–Wilk test); \(\Delta\), root mean-square deviation.
percentage of explained variance) but with very different estimations, when different
starting values are used. For example, setting all starting values at 0.001, the first parameter
in the equation (i.e. the asymptote) is calculated as 4109.430 (variance explained:
65.76%), whereas setting all staring values at 0.0001, the first parameter in the equation is
calculated as 645.497 (variance explained: 65.97%). Likewise, changing starting values
determined very different parameter estimations for the Lomolino function, and this is a
usual problem for curvilinear algorithms. All curvilinear regressions gave a predicted
number of species for Thasos (ranging from 14.3 to 17.9, according to the model) rather
inferior to the actual one (23). The best predictions were those of the power function,
Weibull three-parameters, and Lomolino’s function. Among the linear models (which gave
predictions ranging from 14.6 to 21.4), the linear function furnished the worst value, the
exponential the best one. Also for linear models, predicted values were inferior to the actual
one.

As a whole, the power function appeared to be the most convenient model. Using the
power function by curvilinear regression gave a higher $R^2$ than the FI of the linearized form.
The $z$ value of 0.260 obtained from the power function in its linear form is very close to that
(0.263) predicted by theory (e.g. Sugihara 1981). By contrast, the $z$ value obtained by the
curvilinear fit was substantially higher ($z=0.41$), possibly a reflection of the stronger
influence of higher values.

However, both these exponent values fall within the range of those typically found in the
species–area relationship ($z=0.2–0.4$), especially for island groups and archipelagos (cf.
Connor and McCoy 1979; Rosenzweig 1995).

Zoogeographical composition of Thasos tenebrionids

Analyses of geographical ranges of the species allowed us to classify them into seven types
of ranges (i.e. areographic groups of species; Table II). Areographic groups of species were
as follows: East Mediterranean, 61%; Mediterranean, 9%; South European, 9%; Sibiro-
European, 9%; Turano-Europeo-Mediterranean, Turano-Mediterranean, and European,
4%. As expected, the East Mediterranean component is the highest because of the eastern
position of Thasos in the Mediterranean. However, all of the species assigned to the East
Mediterranean chorotype are actually restricted to the northern and central sectors of the
East Mediterranean, being absent from the African areas facing the East Mediterranean.
The occurrence of species with wider distributions, some of which are centred in Europe or
in the Sibiro-European area, contrasts against the typically Mediterranean shape of this
fauna.

In terms of their distribution in the Aegean area, most of the species appear to be widely
distributed. A relevant percentage is represented by the Balkan species, while only one is
Anatolian. The prevalence of species widely distributed or Balkan suggests that most of the
immigration of the species must have been of predominantly Balkan origin. Actually, the
prevalence of Balkan species aligns the island among the westernmost ones, characterized
by a high proportion of Balkan species (Figure 2).

Faunal similarity

MS analysis revealed a rather complex pattern, in which however the eastern islands appear
to be well isolated (Figure 3).
DFA produced a good discriminant function (Table V), with only one island (Rhodos) being incorrectly classified. The percentage of Anatolian taxa was identified as being particularly useful in distinguishing between “Balkan” and “Anatolian” islands (Table V).

Based on these results, three main faunal divisions, recognized by zoogeographical discontinuities, can be identified. A first discontinuity crosses the Aegean Sea leaving the eastward islands near the Anatolian coast. A second discontinuity runs between Kriti and the Cyclades. A third discontinuity separates Euboea and Thasos from most of all the other islands.

Parsimony analysis of endemcity

PAE using the Wagner parsimony yielded 12 most parsimonious cladograms (length=342, HI=0.694, CI=0.307, RI=0.482, RC=0.240). The strict consensus tree is shown in Figure 4. All the Anatolian islands are grouped into a single cluster, which however has the Cycladic (Kea (Andros, Paros, Tinos)) cluster as the sister. A basal, poorly resolved cluster of Cycladic islands is also recognizable. This cluster, the sister to all others, includes some Cyclades (i.e. Amorgos, Kithnos, Mikonos, Siros) that were grouped in different basal clades due to uncertain associations with other islands. Thasos is the sister to Euboea, which, along with Anafi, forms a sister clade to a large Cycladic clade. Rather surprisingly, Kriti falls within this Cycladic cluster, as the sister to Naxos, possibly due to the (almost) unique co-occurrence of some rare species with a highly scattered distribution (e.g. Cnemeplatia atropos, Cataphronetis reitteri, G. constatum, G. setulosum, Scleron multistriatum).

PAE using the Dollo parsimony yielded two most parsimonious cladograms (length=512, HI=0.818, CI=0.182, RI=0.829, RC=0.275). The strict consensus tree

![Graph](image-url)
is shown in Figure 5, and it appears preferable to that obtained by the Wagner parsimony. Kimolos, Folegandros, and Skiros appear to occupy a basal position. Some other Cyclades (i.e. Amorgos, Kithnos, Paros, Mikonos, Milos, and Siros) are grouped in different basal clades due to uncertain associations with other islands, as in the previous analysis. In a more derived position, two large clades can be identified: (1) a clade including most of the Cyclades; and (2) a clade including the Anatolian islands with, however, also a derived clade comprising Euboea, Skopelos, and Thasos. Within the first clade, a more derived

Table V. Results of discriminant analysis.

| Standardized coefficients for canonical variables |  |
|-----------------------------------------------|--|
| ANA                                           | 0.767 |
| BAL                                           | -0.476 |
| SUB                                           | -0.311 |
| Eigenvalue                                    | 1.926 |
| Canonical R                                   | 0.811 |
| Wilks' lambda                                 | 0.342 |
| Chi square                                    | 29.522 |
| df                                            | 3    |
| P                                             | 0.000 |

| Correct classifications (%)                   |  |
|-----------------------------------------------|--|
| Group 1                                       | 100.000 |
| Group 2                                       | 87.500 |
| Total                                         | 96.774 |

ANAA, percentage of Anatolian taxa; BAL, percentage of Balkan taxa; SUB, percentage of sub-endemic taxa; Group 1, Balkan islands; Group 2, Anatolian islands.
clade includes Andros, Kea, and Tinos (three islands which are close to each other). As to the clade including Euboea, Skopelos, and Thasos, all of these islands are located in the northern part of the Aegean, near the Greek coast. Note also that Kriti is the sister to a clearly defined clade of south-eastern islands.

Discussion

A positive relationship between area and tenebrionid richness was found using all methods. Connor and McCoy (1979) first suggested that the best-fit model for a particular
species–area curve can usually only be determined empirically. Their observations referred to the linear model and the convex (exponential and power function) models. Recently, the question of whether the species–area relationship is asymptotic has been deeply debated. Lomolino and Weiser (2001) have proposed a possible modification (the break point transformation) for both the exponential and the power functions, to take into account a postulated asymptotic character of the species–area relationship. However, Williamson et al. (2001) denied that the species–area relationship has an asymptote. In response to the latter paper, Lomolino (2002) specified that he used the term asymptote to refer to the boundary which the species–area relationship should have because of the finite nature of the source pool, so that the curve is sigmoidal. Williamson et al. (2002) strongly contested the postulated sigmoidal behaviour of the species–area relationship, stating that the finite number of species defines a point, not an asymptote or a boundary, and that point may theoretically be approached more or less horizontally or more or less vertically or in any diagonal way. More generally, it appears that no model can be considered as paradigmatic, but the actual relationship may be best represented by different models according to the area and the taxon involved.

Figure 5. Parsimony analysis strict consensus tree based on Dollo parsimony. Arrow shows the position of Thasos.
According to Tjørve (2003), sigmoid curve models should be expected to fit isolate (habitat patch or island) data, and convex models should fit sample area (census patch) data. Convex models should also fit isolate-type data where no data are present from the lower convex downward (j-shaped) part of the curve.

For the studied system, the power function represented the best fit model. This suggests that the investigated system apparently conforms more to a census patch condition than isolated areas, or that no data are present from the lower part of the curve. This second explanation appears to be more realistic and can be interpreted as a reflection of the low number of islands with very few species. Williams (1996) pointed out that excluding islands with no species influences the fit, and this consideration applies to the exclusion of islands with few species. For the study islands, no island with zero species has been included, and islands with very low species richness (less than seven species) represent a very reduced sample (three out of 32). This is because we used data collected from a wide range of sources. Thus, we cannot be sure that islands apparently without species, or with very few species, have been as well investigated as the others. In other terms, based on the historical information about biological recording, all islands included in this study have been deeply investigated, but we have been forced to exclude many islands with apparently very few or no species because we are unable to assess if such values are real or derived by under-sampling. Within the power function, the non-linear method appeared superior in terms of $R^2$, but, as also observed by Welter-Schultes and Williams (1999), more strongly influenced by higher values.

The parameters $C$ and $z$ of the power function in its linear form can be easily compared with those calculated for other taxa in the Aegean archipelago. After decades of intensive study of the species–area relationship (e.g. MacArthur and Wilson 1967; Connor and McCoy 1979; Gould 1979; Sugihara 1981; Wright 1981; Crowell 1986; Newmark 1986; Nilsson et al. 1988; Sfenthourakis 1996a; Lobo and Martín-Piera 1999; Welter-Schultes and Williams 1999; Hovestadt and Poethke 2005), the question whether or not the values of $z$ have any importance for ecological communities remains unresolved. Also, if the 0.20–0.40 range is considered as the null hypothesized range of slopes, only slope values deviating from this range should have biological significance (Connor and McCoy 1979). However, a comparative study of $C$ and $z$ values may throw light on some biogeographical aspects. In particular, the estimated parameters $C$ and $z$ of the equation suggest that the tenebrionid fauna of the Aegean Islands is relictual.

Gould (1979) suggested that, when $z$ values 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 linearized power function model for land snails ($S=9.48A^{0.18}$; Welter-Schultes and Williams 1999) and isopods ($S=9.33A^{0.20}$; Sfenthourakis 1996a) can be compared with that observed for the tenebrionid beetles ($S=3.38A^{0.26}$). It appears that $C$ values are higher for snails and isopods than for tenebrionids.

An opposite trend appears for the $z$ value, which is higher for tenebrionids, and lower for isopods and snails. This fits with Lomolino’s (2001) observation that $z$ and $C$ values should be interdependent and an increase in $z$ values must be accompanied by a compensatory decrease in $C$ value.

As to the $C$ values, they show that, regardless of island size, the biota contains about three species of land snails and isopods for each tenebrionid species. This fact may suggest that: (1) tenebrionid species require a greater extent of habitat than land snails or isopods (possibly because of the large size of some species, like 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. Actually, the tenebrionid fauna of the Aegean Islands is mostly composed of apterous species, which therefore have a limited capacity to disperse. 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 is not a consequence of living on islands, but evolved before island colonization. In general, although aptery greatly reduces the beetles’ ability to actively disperse, other dispersal mechanisms, such as rafting and water transport, may produce widespread distributions (cf. Carpaneto and Fattorini 2002) and cannot be a priori discharged as factors assisting island colonization 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 dispersal played an important role in determining their present distribution patterns. However, these processes may involve a limited amount of species, while land connection strongly facilitates island colonization. Therefore, low dispersal animals tend to form relict faunas, and low dispersal ability and relictuality may be viewed as two faces of the same coin.

A possible relictual character of the tenebrionid fauna is also suggested by the higher $z$ value. According to Lomolino (2001), in comparison with samples of mainland biotas, species–area relationships for biotas of isolated islands tend to be more linear (higher values of $z$), but have fewer species per unit area (and, therefore, lower $C$ values than mainland curves) (Lomolino 2001). A higher $z$ value for tenebrionids on the Aegean Islands could therefore suggest that this fauna has a more pronounced insular character than the isopod and snail faunas on the same archipelago, possibly as a consequence of a lower ability in island colonization in tenebrionids. The absence of an isolation effect (i.e. distance to mainland) on species richness reported by Fattorini (2002a, 2002b) may be also considered a definitive proof that the tenebrionids of the Aegean Islands are truly relictual.

Multi-dimensional scaling and cladograms obtained by PAE gave comparable results. In the preferred PAE analysis, Kimolos, Folegandros, and Skiros appear to occupy a basal position, suggesting an ancient isolation. Actually, according to Dermitzakis’ (1990) palaeogeographical maps, Skiros has been separated from both the Balkans and the Anatolian peninsula since the Tortonian. As Kimolos and Folegandros lie on a volcanic area, their fauna could have been subject to strong impoverishment due to volcanic activities, also in the Pleistocene. Thus, it is reasonable to consider that they were re-colonized in recent times by species with high dispersal ability. Species with high dispersal power tend to be widely distributed on all islands, appearing thus as ancient synapomorphies linking areas at basal nodes. More generally, the synapomorphies of basal nodes of PAE cladograms are represented by species that should occur in (almost) all of the considered areas. As they are the most widespread species within a given study set, it is also reasonable to suppose that they are species with high dispersal ability, i.e. taxa-as-characters that can be highly homoplastic. This fact may represent an overlooked source of PAE bias in deducing vicariance events at basal nodes. Other possible problems due to widespread taxa are outlined by Glasby and Alvarez (1999). The particular position of Kriti obtained by PAE under Dollo parsimony may suggest a possible relationship with the other islands of the so-called South Aegean Arch. Actually, some tenebrionid species seem to have distributional patterns which support a faunal relationship among Kriti, the South Aegean Arch and the adjacent mainland areas (Fattorini 2002a). Such distributions could be a result of dispersal events among these areas during Pleistocene regressions, when the distances among the
islands of the South Aegean Arch and the adjacent mainlands were substantially reduced (Dermitzakis 1990), allowing for faunal exchanges followed by vicariance events.

The congruence between PAE and palaeogeographical reconstructions suggests that either vicariance or concerted range expansion (or both) may actually account for tenebrionid distributions in the study area. PAE results grouping the south-eastern islands into a crown clade suggest that their tenebrionid fauna is of monophyletic origin. This fits with geological evidence (Dermitzakis 1990) that these islands were connected to Anatolia, but remained separated from other Aegean Islands throughout the Quaternary. By contrast, the lack of clear hierarchical patterns in the position of many Cyclades may reflect multiple cycles of connection to/disjunction from each other or the mainland areas.

MS, PAE, and DFA strongly support the existence of faunal regions defined by Pleistocene island configurations. In particular, the clear faunal discontinuity between the western and central Aegean Islands on one side, and the islands close to the Anatolian coast on the other, is consistent with the persistence (from Messinian to Pleistocene) of a sea barrier between these two groups of islands. The separate position of Kriti is also confirmed.

All these results suggest that most of the tenebrionid species have probably colonized the Aegean Islands by means of land-bridges during 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. 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 and Sondaar 1981; Dermitzakis 1990; Sfenthourakis 1996a; Welter-Schultes and Williams 1999, and references therein). In particular, according to Dermitzakis (1990), Kea was connected to Euboea, in turn connected to the Balkan coast. Skopelos remained isolated from most of the islands, being only joined with the adjacent North Sporades. Kimolos and Milos were connected to each other, but remained isolated from other Cyclades. Sifnos, Serifos, and Thasos also remained isolated. Lemnos was connected to adjacent minor islands and its distance to the Balkan coast was greatly reduced. Most of the Southern Sporades were connected to each other and to the Anatolian coasts. Rhodes remained isolated, while Karpathos was connected to Kassos. A wide sea barrier existed between the Cyclades and the eastern islands. Tenebrionid species with very low dispersal abilities may have reached a continuous distribution between mainland and present island 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.

Based on these palaeographical Pleistocene scenarios, we can suppose that the Aegean Islands were subject to a twofold colonization process. Many Balkan elements could have easily reached the Cyclades and Northern Sporades, but not the Southern Sporades, due to the persistence of the sea barrier. In contrast, Anatolian species could have easily reached the eastern islands, but not the central Aegean and the western ones. Obviously, as over-sea dispersal cannot be completely discounted, an overall transitional character is expected. In addition, over-sea dispersal has surely to be implied in the colonization of Pleistocene island groups that were not connected to the mainland. However, if dispersal is reduced, a homogeneous distribution of Balkan and Anatolian species is not expected. Actually, the proportion of Balkan taxa sharply decreases from west to east, whereas the Anatolian taxa
follow an opposite trend. Also, as far as faunal composition is concerned, the palaeogeographic scenario reported above suggests the occurrence of two main districts separated by a line crossing the sea west of the eastern Aegean Islands and north of Kriti.

In contrast with most of the other islands, the fauna of Thasos is probably strongly affected by dispersion from the adjacent mainland. Thasos clustered with Euboea, which is separated from the mainland by only about 300 m and which can therefore be considered more a Balkan peninsula than a true island. However, there are some islands that are closer to the mainland than Thasos but which clustered with other truly isolated islands. In other words, Thasos seems to harbour a fauna quite similar to that of the mainland without obvious relationships with other islands. This can be explained by different reasons. First, Thasos is closer to the mainland than to any other island. Thus, Thasos did not have direct faunal exchanges with other islands. Possible Pleistocene faunal immigration could have taken place from the adjacent Balkan mainland, while the island did not have connections to other islands. According to the maps of Dermitzakis (1990) and Welter-Schultes and Williams (1999), Thasos remained isolated from the mainland during glaciations, but from maps in Durand et al. (1999) it appears connected during the Pleistocene. Let us remark that the isolation of Thasos, as represented in the maps of Welter-Schultes and Williams (1999), contrasts with the present day 100 m isobaths, which suggest that, during glacial lowering in sea level, the island was connected to the mainland. In any case, it is reasonable to assume that during the Pleistocene the distance between Thasos and the mainland coastline was reduced, favouring colonization processes. Second, the island could be subject to colonization from the mainland by dispersal more than other islands. Winds in the Aegean strongly influence wave direction and force according to two major patterns (Christopoulos 1997): (1) in summer dry winds of northern sectors, from North to South, prevail; (2) in winter, the Aegean is the site of violent wind storms both from North to South and from South to North. In this context, according to the maps of Christopoulos (1997), Thasos appears mostly affected by winds, and therefore waves, from North to South. This pattern may facilitate a high rate of dispersal from the mainland to the island by aerial propagulae, especially in the case of small-sized (and sometimes winged) species, such as *A. rufus*, *Catomus consentaneus*, or *Nalassus plebejus*, as well as rafting and water transport (especially for species living in littoral habitats, such as *Dendarus* spp., *Gonocephalum* spp., *Opatrum* spp., *Tentyria rotundata*, *X. graecus*, *Zophosis punctata*, as well as *A. rufus* and *C. consentaneus*).

The high number of taxa occurring on Thasos (23 plus *Blaps gigas*) reinforces the idea that the island benefits from present-day dispersal from the adjacent mainland. The species number for Thasos is much higher than would be expected from its area alone using all the applied functions. It could be postulated that most of the islands have their species number regulated by Pleistocene colonization, and this determines the species–area relationship from which Thasos positively deviates because of a species number “anomalously” enhanced by a higher incidence of present dispersal. From this point of view, Thasos, in contrast with most of the Aegean Islands, appears to have a more equilibrial than relict fauna.

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, anthropogenic pressures, or the presence of sandy beaches, may have concurred to determine the present-day island tenebrionid richness on each island.
For the island of Thasos, greater habitat diversity may be also responsible for the “exceptionally” high number of species. The occurrence of wooded areas (presently strongly reduced by man on many islands) is an important factor for those species associated with trees such as Platydema europaeum, B. reticulatus, Helops rossii, Menephilus cylindricus, and Nalassus plebejus. The presence of well-preserved sandy-shores and dunes is crucial for psammophilic species like A. rufus, Catomus consentaneus, O. obesum, O. sabulosum, and X. graecus.

Conclusions

The fauna of each of the Aegean Islands can be divided readily into two groups: one consists of western species, i.e. species that colonized the islands from the Balkan fauna; the other of eastern species, i.e. those colonizing the islands from the Anatolian peninsula. These two groups show opposite distribution patterns. The Balkan elements decrease from west to east, while the Anatolian elements decrease from east to west, thus allowing for an overall transitional character for the tenebrionid fauna. Such a pattern can be a priori consistent with both present geography and past land configuration. However, some evidence supports the hypothesis that palaeogeographical factors are strongly involved in determining present distributional patterns.

First, in terms of colonization patterns, the tenebrionid fauna does not follow equilibrial models. Second, the tenebrionid fauna of the Aegean Islands appears to be composed of structured species assemblages. In particular, a clear faunal discontinuity can be observed between the eastern islands and the western ones. This discontinuity, revealed by a multi-method statistical approach, is also consistent with results obtained by Parsimony Analysis of Endemicity.

The first point agrees with the results obtained by Welter-Schultes and Williams (1999), who demonstrated a relict character for the land snail fauna of the Aegean Islands. As to the second point, Sfenthourakis (1996a) observed an important discontinuity between western and eastern islands for the oniscid fauna of the Central Aegean. The present paper agrees with these findings, extending and defining the importance of this barrier. Also, this study revealed twofold colonization involved in the tenebrionid distribution, resulting in an overall transitional character for this fauna. However, as a result of palaeogeographical configurations, there is not a homogeneous gradient, but the eastern islands are characterized by a typical Anatolian fauna while Balkan species predominate in the western ones.

Thasos clearly belongs to the Balkan group, but with some Anatolian influence. From an idiographic point of view, Cephalostenus orbicollis shows a particular distribution pattern that deserves some comment. This species has been repeatedly confused with C. elegans (Brullé, 1832), from which, however, it can easily be distinguished by the elongate shape of the male head. The Thasos population belongs to C. orbicollis and earlier records of C. elegans from the island have to be referred to this species also. C. elegans and C. orbicollis appear to be vicariant taxa. C. elegans occurs in the Balkans and on the Ionian Islands (not on the Aegean Islands), while C. orbicollis occurs in Anatolia and on the Aegean Islands. This pattern is singularly paralleled by the snake-eyed lizard Ophisops elegans Ménétries, 1832, which occurs in Anatolia as well as European Turkey and on some Aegean Islands, including Thasos (Kühnelt 1986; Sindaco et al. 2000).

In accordance with the East Mediterranean location of Thasos, most of the species appear to be more or less widely distributed in the Mediterranean basin, with a high
proportion of East Mediterranean elements. Obviously, species with such type of
distribution are also typically thermophilic species, associated with the Mediterranean
maquis. Therefore, the climate of the study area, favouring species with thermophilic
preferences, can be responsible for a high incidence of species with such ranges. As
evidence of this fact, the Mediterranean elements are mostly represented by sand-dwelling
thermophilic species.

Species with more northern distributions (e.g. European, South European or Sibiro-
European species) are relatively scarce, including some euryoecious or xylophilous
elements. The presence of species with such ranges can be related to the occurrence of
relict patches of mesophilic vegetation. Most probably, such species largely colonized the
Mediterranean coastal areas during Pleistocene glaciations, as a consequence of a more
temperate climate that favoured the dispersal of mesophilic species from northern and
inland regions to southern and coastal areas. As the climate became drier and warmer,
these species were forced to assume more northern distributions. However, isolated
populations were able to survive in areas like Thasos, where favourable habitats persisted.
Therefore, these relict populations are a result of dispersal/vicariance events determined by
the fragmentation of mesophilic habitats that were widespread also over coastal areas
during Pleistocene glaciations.

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