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Spatial patterns of diversity in the tenebrionid beetles (Coleoptera, Tenebrionidae) of the Aegean Islands (Greece)

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ABSTRACT

Question: How do present and historical factors influence beta and gamma diversity of strictly resident animals on a land-bridge archipelago?

Data description: Islands were characterized in terms of present geography, shape, area size, habitat diversity and paleogeography. Diversity patterns are based on 170 tenebrionid taxa from 32 islands (Greece).

Search method: The influence of present eco-geographic variables on gamma diversity (species numbers) was assessed using pairwise correlations, multiple regressions and path analysis. Canonical correspondence analysis was applied to study the influence of present and past island characteristics (represented by multidimensional spaces) on beta diversity (calculated as biogeographic similarity among islands). Fuzzy analysis was applied to determine island groupings based on beta diversity.

Conclusions: Larger islands have more species because they have more habitats. Distance and shape effects were small. Thus present colonization processes do not play a substantial role. Tenebrionids colonized the islands by Pleistocene land-bridges. Larger islands retained more species. Beta diversity was moulded mostly by paleogeographic conditions. The Aegean Islands were subject to a twofold colonization process. Relatively few species have been able to cross the middle Aegean sea barrier to colonize islands far from their mainland source.

Keywords: beta diversity, gamma diversity, island biogeography, land-bridge islands, paleogeography.

INTRODUCTION

Although transitional areas are of extremely high biogeographic interest, they are very hard to study, because of the puzzling distribution of species, which makes it difficult to clearly understand the present and past factors responsible for such complex patterns (e.g. Cowie, 1989; Krasnov and Shenbrot, 1996, 1998; Morrone and Márquez, 2001; Sans-Fuentes and Ventura, 2000; Nogués-Bravo and Martínez-Rica, 2004).

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The Aegean Islands have long been recognized as an important transitional area in the Mediterranean, where Balkan and Anatolian elements overlap (e.g. Aspöck, 1979; Oosterbroek, 1993; Dennis *et al.*, 2000; Fattorini, 2002a, 2002b; Gantenbein and Largiadèr, 2002; Tilmans, 2002), making this archipelago of great biogeographic interest and one of the best studied in the Mediterranean (Beutler, 1979; Simberloff, 1986a, 1986b; Dermitzakis, 1990; Olivier, 1993; Legakis and Kypriotakis, 1994; Sfenthourakis, 1996a, 1996b; Fattorini *et al.*, 1999; Foufopoulos and Ives, 1999; Sfenthourakis *et al.*, 1999, 2004; Welter-Schultes and Williams, 1999; Fattorini, 2000, 2002a, 2002b; Dennis *et al.*, 2000, 2001; Sfenthourakis and Legakis, 2001; Welter-Schultes, 2001; Tilmans, 2002; Chatzimanolis *et al.*, 2003). The present research was undertaken to establish if some general distributional pattern can be recognized in the tenebrionid beetles (Coleopetera, Tenebrionidae) of the Aegean Islands and to elucidate the underlying present (eco-geographic) and historical (paleogeographic) factors. I choose the tenebrionids for four main reasons. First, tenebrionids are an important group in the structure and functioning of Mediterranean insular biotas (Cartagena and Galante, 2002). Second, the tenebrionid fauna of most of the Aegean Islands is well known as a result of intensive surveys from the beginning of the past century to the present (cf. Fattorini *et al.*, 1999; Fattorini, 2002a, 2002b; Leo and Fattorini, 2002). Third, thanks to their highly diversified ecology, tenebrionids are ideal subjects for studies of ecological biogeography, also in island habitats, where these insects are specious while other animal groups have low diversity. Finally, most of the Aegean tenebrionids are characterized by aptery. Species living on islands often lose the ability to disperse (Filin and Ziv, 2004). However, the Aegean tenebrionids evolved aptery before island colonization: the same apterous species which live on islands also occur in the adjacent mainland areas (i.e. Greece and Anatolia) or, if endemic, belong to apterous genera (cf. Fattorini *et al.*, 1999). As vagility of apterous beetles is considerably reduced by their inability to fly (Brühl, 1997), tenebrionids as a group are of great interest in historical biogeography (Fattorini, 2000). In particular, as apterous tenebrionids have an extremely limited ability to actively disperse over the sea (cf. Palmer 1998), they are of particular interest in insular biotas notably affected by historical (vicariant) events like the Aegean Islands (cf. Dermitzakis, 1990; Olivier, 1993; Sfenthourakis, 1996a; Welter-Schultes and Williams, 1999).

Indeed, Fattorini (2002a) found that, on the basis of shared tenebrionid species, islands could be grouped by cluster analysis and parsimony analysis of endemicity into meaningful groups which strictly paralleled the geographic relationships among islands and between islands and adjacent mainlands during the Plio-Pleistocene. Interestingly, such analyses revealed a clear faunal discontinuity between the islands that were connected to the Greek mainland (but not with Anatolia) during Pleistocene falls in sea level, and those that, in contrast, were connected to the Anatolian mainland and not with mainland Greece. Indeed, the Aegean Islands experienced a complex paleogeographic history. In the Langhian (16.5 Ma), the Aegean formed a continental area covered by woodlands with fluvial channels and some freshwater lakes (e.g. Kissel and Laj, 1988; Ten Veen and Meijer, 1998). Massive marine ingressions, caused by crustal stretching, occurred in the Tortonian (9 Ma) onwards. This created the Aegean Sea. The highlands of the former Aegean landmass have never been submerged and some of these mountain peaks were periodically reconnected to the present-day Greek or Anatolian mainlands. The landscape at 7 Ma, before the salinity crisis, is described as an alternation of wooded and bushy areas with some grassy habitats (Merceron *et al.*, 2005), not much different from the Langhian.

In the Messinian, the Mediterranean basin desiccated for 0.3–0.6 million years (Riding *et al.*, 1998; Butler *et al.*, 1999), but never dried out. Lagoon sediments were deposited under sebkha conditions (Giusti and Manganelli, 1984).

According to currently accepted paleogeographic reconstructions (e.g. Dermitzakis, 1990; Olivier, 1993; Sfenthourakis, 1996a; Welter-Schultes and Williams, 1999; Dennis *et al.*, 2000; Cameron *et al.*, 2000, and references therein), the extensive exposure of land resulting from lowered sea levels during the Pleistocene glacial maxima (1.8–0.018 Ma) resulted in the connection of many Aegean Islands to each other and/or to the mainland (Fig. 1). Most of the Cyclades were connected to one another, and their distances to the Balkan coasts were generally reduced or disappeared, while the islands near the Anatolian coasts were connected to the Anatolian mainland. Rhodos remained isolated, while Karpathos was connected to Kassos. A wide sea barrier existed between the Cyclades and the eastern islands. This paleogeographic reconstruction did not substantially differ from that of the Pliocene.

The paleogeographic history of Kriti deserves some additional details. Tortonian marine ingressions resulted in the separation of six or more islands in the area of the Langhian Aegean landmass corresponding to the region of present-day Kriti. These Cretan paleo-islands were relatively stable during the following 7–9 million years. A landbridge of Kriti to the mainland(s) in the Messinian is questionable. During the Pliocene, the Cretan region underwent tectonic uplift of more than 700 m and at least since the Zanclean (4 Ma) the paleoislands were slowly reconnected to one another. This process was completed at 2 Ma.

Fig. 1. Map of the study area. Studied islands are in black. 1: Amorgos, 2: Anafi, 3: Andros, 4: Castellorizon, 5: Chios, 6: Euboea, 7: Folegandros, 8: Ios, 9: Karpathos, 10: Kea, 11: Kimolos, 12: Kithnos, 13: Kos, 14: Kriti, 15: Lemnos, 16: Lesvos, 17: Mikonos, 18: Milos, 19: Naxos, 20: Pano Koufonissi, 21: Paros, 22: Rhodos, 23: Samos, 24: Santorin, 25: Serifos, 26: Sifnos, 27: Sikinos, 28: Siros, 29: Skiros, 30: Skopelos, 31: Thasos, 32: Tinos. Bold line indicates Pleistocene coastline profile at glacial maximum. Modified and combined from Dermitzakis (1990), Sfenthourakis (1996a), Chatzimanolis *et al.* (2003) and references therein.

Therefore, there were three main periods in which present-day islands were connected to each other and/or with the mainlands: (1) before the formation of the Aegean Sea (when present-day islands were mountain highlands), from the Langhian (16.5 Ma) to Tortonian (9 Ma); (2) during the Messinian salinity crisis (6 Ma); and (3) during Pliocene and Pleistocene falls in sea level (2.0–0.2 Ma).

In this paper, however, I concentrate on the possible influence of Plio-Pleistocene land configurations. Biogeographic and evolutionary considerations suggest that pre-Pliocene paleogeography played a less detachable and likely less important role in moulding present distributional patterns.

Many species already lived in the area of the Aegean landmass before 10 Ma and one could postulate that present-day faunal similarity among islands and/or mainlands could be a reflection of this ancient land configuration. According to such a model, tenebrionid species could have continuous ranges over the entire Aegean area, which was fragmented by marine ingressions. However, if the Langhian paleogeography were largely responsible for present-day faunal similarity among islands, one could expect a rather uniform distribution of species among Greece, islands and Anatolia, because all of these areas were connected to each other forming a unique landmass. The existence of a faunal discontinuity in the Aegean between the islands close to Greece and those close to Anatolia contrasts with this possibility, suggesting that most of present-day patterns originated at least after the Tortonian marine ingressions.

During the Middle Miocene and in the Messinian, the Cyclades were connected to the Greek mainland, and the islands near the Anatolian coast to the adjacent mainland, while a wide sea barrier separated these two island groups. This scenario is compatible with the biogeographic similarities among islands found by Fattorini (2002a). However, according to such a model, we should postulate that present-day species ranges originated from the Pliocene fragmentation of these Miocene landmasses. Thus, present endemic species should have evolved allopatrically as a consequence of Pliocene marine ingressions which fragmented such landmasses. There is no available genetic analysis of the Aegean tenebrionids, and phylogeographic studies in Mediterranean beetles are scarce, but some lines of evidence suggest that this process cannot be evoked as the main driving force in the structuring of present distributional patterns. Detailed analyses based on the molecular clock of several tenebrionid species of the volcanic Canary Islands (Juan *et al.*, 1996a, 1996b) showed that they radiated during the last 8 million years, with most of the clades originating from 5 to 0.6 Ma. Similarly, time estimates for genetic divergence among species of the carabid genus *Percus* in Sardinia are quite recent, ranging from the Early Pliocene to the Pleistocene (Ketmaier *et al.*, 2003). Thus, it is likely that most of the present-day tenebrionid species evolved in the Aegean after the Messinian salinity crisis. Since most of the species occurring on the islands are also distributed in the adjacent mainlands, it is likely that they colonized the island from the mainland during the Plio-Pleistocene. The alternative hypothesis of a Miocene continuous distribution fragmented by Pliocene ingressions should have produced remarkable genetic differences, morphologically appreciable at least as species-specific characters. Also, most of the tenebrionid taxa endemic to single Aegean Islands, or to groups of close islands, are presently classified as subspecies of species widespread on the adjacent mainland(s), or as species morphologically very close to each other (cf. Koch, 1948). Thus, it is more reasonable to suppose that they evolved allopatrically by post-Pliocene island isolation, than by pre-Pliocene landmass fragmentation. This does not imply that previous land configurations did not affect in any way present distribution patterns, but Pleistocene regressions appear to be the most relevant paleogeographic factors.

On the basis of these paleogeographic scenarios, and with special reference to the Pleistocene, we can suppose that the Aegean Islands were subject to a twofold colonization process. Many Balkan elements could easily have 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 islands. Finally, Kriti is expected to have evolved a rather unique fauna because of its prolonged isolation and ancient fragmentation into several islands.

Several studies have considered Pleistocene land configuration to be an important determinant of species distribution patterns for sedentary animals like reptiles (Beutler 1979; Foufopoulos and Ives, 1999), land snails (e.g. Heller, 1976; Sfenthourakis *et al.*, 1999; Welter-Schultes and Williams, 1999) and isopods (Sfenthourakis, 1996a; Sfenthourakis *et al.*, 1999), while contemporary geography determines present butterfly distributions (Dennis *et al.*, 2000). However, the possible role of Pleistocene paleogeography on present distribution patterns has been only marginally tested statistically (Hausdorf and Hennig, 2005). The aim of this study was to assess statistically if present-day tenebrionid distribution patterns are affected more by Pleistocene paleogeography or by current geography.

To quantify the local distribution of species, similarity among local species assemblages and rate of change in species composition with respect to present or past conditions, a useful tool is to recognize several ‘levels’ of components of diversity. Two main levels are usually considered in biogeographic research: beta and gamma. Beta diversity measures the rate of change between sites, whereas gamma diversity pertains to the number of taxa at the regional scale (Arita and Rodríguez 2002). Thus, distributional patterns in terms of gamma diversity refer to variation in number of taxa among islands, while distributional patterns in terms of beta diversity refer to variation in similarity (or dissimilarity) among areas (e.g. Magurran, 1988).

In equilibrial archipelagos, the distance to the mainland should have a strong effect on gamma diversity. According to the dynamic equilibrium model of island biogeography proposed by MacArthur and Wilson (1967), immigration rates are enhanced by an island proximity to a source of species (e.g. a mainland area), and large islands have lower extinction rates than smaller islands (an effect of area *per se*) because their larger populations are less vulnerable to stochastic events. Two main predictions follow: (1) the number of species will increase with area, and (2) species richness will decrease with distance, a condition actually found in the Aegean butterflies (Dennis *et al.*, 2000).

According to a relict model, a positive species–area relationship may result from area-dependent extinction or relaxation (cf. Crowell, 1986). Islands could have harboured, and retained, more or fewer species according to their area size and habitat availability. Thus, habitat diversity should be important in determining tenebrionid gamma diversity, because the islands with greater habitat diversity could have retained more species after colonization, while present distance should have negligible effects.

Many other present geographic variables, especially if related to island paleogeography, may exert some influence on present beta diversity. According to the Pleistocene model hypothesized above, one could expect that land-bridge connections should substantially influence present beta diversity, which, in contrast, should be not substantially affected by present geography and ecology.

The aim of this paper was to test statistically the importance of present (geographic and ecological) versus past (paleogeographic) factors in determining present variations in tenebrionid beta and gamma diversity in the Aegean area.

MATERIALS AND METHODS

Study area

The Aegean Islands are situated in the Eastern Mediterranean, between the Greek and Turkish coasts (Fig. 1). The climate of the Aegean Islands is typically Mediterranean. Today, outside the cultivated areas and scattered forest fragments, maquis and phrygana constitute the predominant vegetation types in the Aegean area below the subalpine zone (~1500 m). The two vegetation types frequently intermingle in small-scale mosaics determined mainly by soil properties and moisture regime, and there are intergradations between them. Pre-Minoan Crete held significantly more woodland than it does today, but remains of plants typical of phrygana and maquis are found in interstadials of the last glaciation (Cameron *et al.*, 2000). The Cyclades have been inhabited for at least 4500 years and most arable land was cleared and hillsides terraced over two millennia ago.

As a general rule, while forests were seriously affected by human activities, maquis habitats are relatively well preserved and the phrygana has been greatly extended as a result of deforestation (cf. Simberloff, 1986a; Olivier, 1993). Thus human activities may have caused the extinction of a few tenebrionid species associated with forest habitats. However, the influence of mankind on flora and fauna in Greece, notably on the islands, has never been as strong as during the last 40 years (cf. Papanastasis and Kazaklis, 1998). I used collection data ranging from the end of the eighteenth century to the present time. The vast amount of data available before 1960 (see Fattorini *et al.*, 1999), thus predating the strongest human exploitation of the Aegean area, ensures that the presence/absence data used in this study were not profoundly affected by human influences. 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 which could be absent on some islands, not because of biogeographic reasons but as a result of extinction that occurred in the last decades, is not expected to have any substantial influence on the overall patterns.

Data sources

A total of 32 Aegean Islands were included in this study (Fig. 1, Table 1). On the Aegean Islands, several tenebrionid species are represented by different subspecies endemic to individual islands or groups of islands. On the whole, about 32% of species and subspecies are endemic to the archipelago, suggesting that patterns of tenebrionid distribution and diversity in the archipelago are established over evolutionary time. Most subspecies appear morphologically very close to each other, but usually are distinguishable based on certain characters (cf. Koch, 1948). Moreover, there is an indication that several populations presently acknowledged as subspecies represent profoundly differentiated populations. For example, a recent taxonomic work on the genus *Dendarus* elevated most of the populations previously considered as subspecies to the status of true species which originated as a consequence of a Pleistocene radiation (Chatzimanolis *et al.*, 2002).

Table 1. Tenebrionid beetle richness and eco-geographic parameters from each of the 32 evaluated Aegean Islands

Island	*S*	*A*	*La*	*Lo*	*E*	*Di*	*Dm*	*P*	*NH*
Amorgos	7	121.1	36.50	25.59	821	12.8	104	112	10
Anafi	12	38.4	36.21	25.50	582	20.8	140	32	12
Andros	13	380	37.45	24.42	994	2	57	177	16
Castellorizon	8	7.3	36.08	29.34	271	120.8	2	19	8
Chios	10	842	38.22	26.00	1297	20	11	213	9
Euboea	42	3658	38.34	23.50	1745	11.2	0.3	678	30
Folegandros	7	32.1	36.37	24.54	415	14.4	132	40	16
Ios	9	107.8	36.42	25.24	713	6.6	147	81	—
Karpathos	15	301	35.40	27.10	1215	1	93	160	14
Kea	6	130.6	37.34	24.22	560	8.8	20.5	81	6
Kimolos	3	35.7	36.48	24.34	358	1.2	102	38	13
Kithnos	4	99.3	37.25	24.28	306	8.8	36	98	8
Kos	26	290.3	36.50	27.10	843	4	3.5	112	19
Kriti	71	8260	35.29	24.42	2456	36.8	99	1046	54
Lemnos	10	460	39.54	25.21	459	24	59	259	12
Lesvos	17	1630	39.10	26.20	968	51.2	10.5	370	20
Mikonos	10	85.5	37.29	25.25	372	2.4	114	81	—
Milos	19	150.6	36.41	24.15	751	1.2	100	126	16
Naxos	36	428	37.02	25.35	1001	5.8	130	148	14
Pano Koufonissi	12	3.8	36.56	25.59	114	0.6	147	15.3	11
Paros	8	194.5	37.08	25.12	705	1.6	116	118	5
Rhodos	43	1400	36.10	28.00	1215	8.2	21	220	12
Samos	14	476.2	37.48	26.44	1434	5.6	2.8	159	21
Santorin	26	31	36.24	25.29	586	20.8	173	69	10
Serifos	8	73.2	37.11	24.31	585	12	64	81	12
Sifnos	9	73.2	36.59	24.40	678	12	87	70	10
Sikinos	8	41	36.39	25.06	533	6.6	144	41	—
Siros	23	83.6	37.26	24.54	422	16.8	75	87	10
Skiros	11	209	38.53	24.32	792	52	75	130	9
Skopelos	7	96	39.10	23.40	680	3.2	21	67	20
Thasos	23	379	40.41	24.47	1203	57.6	6	95	2
Tinos	13	194.3	37.38	25.10	730	8	80	106	12

Note: *S* = Tenebrionid richness (number of species and subspecies), *A* = area (km^2), *La* = latitude (°N), *Lo* = longitude (°E), *E* = elevation (metres above sea level), *Di* = distance to the nearest island (km), *Dm* = distance to the nearest mainland (km), *P* = perimeter (km), *NH* = number of habitats (—, islands without 'Natura2000' sites).

For these reasons I have counted populations, presently recognized as subspecies, as different taxa. For simplicity, the term 'species' will be used to refer to tenebrionid taxa. Data regarding species distributions 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 to be valid) and in various nomenclatorial changes. Taxonomy and faunistics of the genus *Asida* were 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 *Xanthomus* *cyprius* (Ferrer and Whitehead, 2002) was also noted. Finally, records of *Gonocephalum affine* and *G. setulosum* from Kriti (Ferrer, 1995) were added. Faunal records for Thasos were updated according to new data (S. Fattorini and A.P. Fowles, in prep.), which include first records of *Ammobius rufus*, *Bolitophagus reticulates*, *Diaclina fagi*, *Dichillus carinatus*, *Gonocephalum granulatum nigrum*, *Helops rossii*, *Nalassus plebejus*, *Opatrum obesum* and *Platydema europaeum*.

I have omitted synanthropic (and hence possibly introduced), transient, exotic or poorly known species (cf. Fattorini *et al.*, 1999). The very slight differences between the numbers of taxa recorded here [which include a vast number of recent records (cf. Fattorini *et al.*, 1999)] and those quoted several years ago by Dajoz (1987) suggest that future increases in species numbers will not be substantial.

As a whole, 170 taxa (138 species and 32 subspecies) were ascertained to occur as native populations on the study islands.

Data analysis

Effect of island size and habitat diversity

One of the most controversial issues in island biogeography is the importance of habitat diversity and area *per se* in determining species number (Kohn and Walsh, 1994; Ricklefs and Lovette, 1999; Davidar *et al.*, 2001). As habitat diversity and area tend to be interrelated, it is very difficult to distinguish their different contribution in determining species richness. In this study, I used two measures of habitat diversity and two different approaches.

The most frequently employed diversity measure is maximum elevation (Ricklefs and Lovette, 1999; Schoener *et al.*, 2001). As elevation is correlated with temperature, precipitation, humidity, wind speed, evaporation and insulation, it may be an indirect, 'universal' measure of habitat diversity (cf. Fattorini, 2000; Kocher and Williams, 2000). However, as elevation is an indirect measure, increases in elevation cannot be considered a true consequence of increasing area, because there is a correlation but not a causal relationship between area and elevation. For this reason, I used an additional, direct measure of habitat diversity for the analyses specifically devoted to the study of the differential contribution of habitat diversity and area in predicting species number on islands. As a direct measure of habitat diversity, I used the number of habitats occurring on islands (Kohn and Walsh, 1994; Sfenthourakis, 1996a; Ricklefs and Lovette, 1999).

I referred here to the classification of habitat types reported in Annex I of the 'Habitat Directive' (92/43/EEC), as implemented in the project 'Inventory, Identification, Evaluation and Mapping of the Habitat Types and Flora and Fauna Species in Hellas' (Habitat Committee 3–4/6/94 and Life Committee 5–6/10/94). In particular, most of the Aegean Islands contain one or more proposed 'Natura 2000' sites, for which a detailed list of habitats is provided by the Hellenic Ministry for the Environment, Physical Planning and Public Works (http://www.minenv.gr: accessed March 2004). I checked all proposed sites on each island. The full array of habitat types listed for all sites recorded in each island was then considered as a measure of habitat diversity. This classification appears adequate because it is sufficiently detailed with respect to the possible array of habitats exploited by tenebrionids. I omitted some habitats which are clearly not relevant for tenebrionids, like *Posidonia* beds, reefs and submerged or partly submerged sea caves. The islands of Ios, Mikonos and Sikinos were omitted because no 'Natura 2000' site was designated for them.

Path analysis allows the relative direct and indirect effects of casual (or predictor) variables to be assessed, according to an *a priori* model and subject to several assumptions (cf. Kohn and Walsh, 1994; Stevens, 2004). To evaluate the relative importance of area (A) and number of habitats (NH) in determining species richness (S), I performed a multiple regression of S on A and NH (cf. Kohn and Walsh, 1994; Sfenthourakis, 1996a; Ricklefs and Lovette, 1999). The actual shape of this multiple relationship cannot be determined on theoretical grounds and several models, based on different axis log-transformations, have been applied (Kitchener *et al.*, 1980, 1982; Reed, 1981; Torres and Snelling, 1997). I tested all regression models using S, A and NH – and their $\log_{10}$-transformed values – in all possible combinations. The only multiple regression model for which both area and number of habitats entered as significant variables was $S = C + a\log A + bNH$, where C is a constant. Thus, I selected this model to explore the contribution of A and NH in determining S. As in general NH is related to A, I tested this possible correlation with different models. The equation $NH = C + a\log A$ adequately linearized the relationship, and the correlation coefficient of this model was retained as the most appropriate for the following path analysis.

The appropriate path model for the effect of area and habitat number upon species richness per island is shown in Fig. 2. The path coefficients a_1, b_1 and b_2 represent direct effects of one variable on another: a_1 is the simple correlation coefficient for the variables habitat number and area as obtained from the regression $NH = C + a\log A$; b_1 and b_2 are the standardized regression coefficients (β) from the multiple regression model $S = C + a\log A + bNH$. Indirect effects are calculated as the product of the path coefficients along the links between causal variables and the response variable through other causal variables. Effect coefficients are the sum of direct and indirect effects (see Results).

The same procedure was applied using elevation (E) as a measure of habitat diversity. I tested all possible regression models using S, A and E – and their $\log_{10}$-transformed values – in all possible combinations. In this case, the only multiple regression model that included both area and elevation with significant correlation coefficients was $\log S = aA + b\log E$. Thus this equation was used to develop this path analysis.

Analyses were performed using Statistica software (version 4.5, 1993).

Effects of present geography on gamma diversity (species richness)

To study the possible influence of present island characteristics on gamma diversity (species number S on different islands), I considered the following geographic variables: area (A), latitude (La), longitude (Lo), elevation (E), island perimeter (P), distance to the mainland (Dm) and distance to the nearest island (Di). Latitude and longitude were converted from degrees and minutes to decimal format using the formula: degrees + (minutes/60). The influence of these variables on species richness was assessed by multiple regressions.

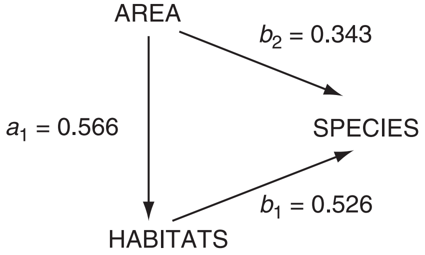

Fig. 2. Path model and path coefficients of species number as a function of area and habitat number. Island area directly affects habitat number and both area and habitat number directly affect species per island.

Although habitat number and elevation were used alternately in the path analysis, for various reasons I did not use number of habitats as an additional or alternative measure of habitat diversity in these multiple regressions. First, if habitat number is added as another measure of habitat diversity, redundancy prevents the inclusion of area as a significant variable. In fact, area is correlated with both number of habitats (Spearman's $r_s = 0.380$, $P < 0.05$, $N = 29$) and elevation ($r_s = 0.844$, $P < 0.001$, $N = 32$); therefore, although area is a strong predictor of species richness, it is excluded from a stepwise regression model owing to its high correlation with these two other, albeit stronger, predictor variables. Second, the variables elevation and number of habitats were correlated ($r_s = 0.419$, $P < 0.05$, $N = 29$), so they could be used as alternative measures; however, elevation is a measure available for all islands involved in the analysis, while number of habitats was not available for three islands (Ios, Mikonos and Sikinos), making elevation the preferred variable.

Generally speaking, most environmental variables are spatially structured and therefore are autocorrelated. This implies a lack of independence among the observations and creates problems with tests of statistical significance. Species richness is obviously suspected to have a spatial structure determined by coordinates (latitude and longitude). I regressed species richness against the third-degree polynomial of the latitude (X) and longitude (Y) of each island [trend surface analysis, TSA (Legendre, 1993)] by both forward and backward procedures:

$$y = f(X, Y) = b_0 + b_1 X + b_2 Y + b_3 X^2 + b_4 XY + b_5 Y^2 + b_6 X^3 + b_7 X^2 Y + b_8 XY^2 + b_9 Y^3$$

Since none of the spatial terms were significant, species richness is not affected by spatial structure.

The relationship between species richness and environmental variables is often curvilinear (Austin, 1980). However, it is known that logarithmic transformations tend to linearize many monotonic increasing functions (Haila, 1983). Also, for most of the variables used in this study, log-transformations increased normality (Shapiro-Wilks W-test) (Fig. 3), and since the relationship between two normally distributed variables is necessarily linear, using log-transformed variables could have increased the efficiency of the multiple linear regressions. For these reasons, both species richness and all geographic variables were $\log_{10}$-transformed. A forward stepwise multiple regression has been used for ranking the eco-geographic variables in terms of their importance to determine the species number. Note that in this manner, species richness is linked to area according to the well-known power function (cf. Rosenzweig, 1995).

For comparative purposes, I developed another multiple regression using untransformed values of species richness. The Pearson product–moment correlation coefficient was used to estimate the correlations between species richness and these eco-geographic variables (Fig. 3).

To study the possible spatial structure of the geographic variables discussed above, I regressed separately each geographic variable against TSA. Only *Di* and *Dm* showed a significant correlation to spatial terms (to XY and X^2Y respectively). I retained the residuals from these regressions and I used them as an estimate of variables without their spatial structure (cf. Nogués-Bravo and Martínez-Rica, 2004). I then performed new multiple regressions between species richness (raw and log-transformed) and geographic variables using the retained residuals in lieu of *Di* and *Dm*. These regressions yielded results identical to those obtained using *Di* and *Dm* directly. Therefore, the spatial structure in the original variables *Di* and *Dm* did not affect the results, and only the regression between log-richness and log-variables are presented for the sake of clarity.

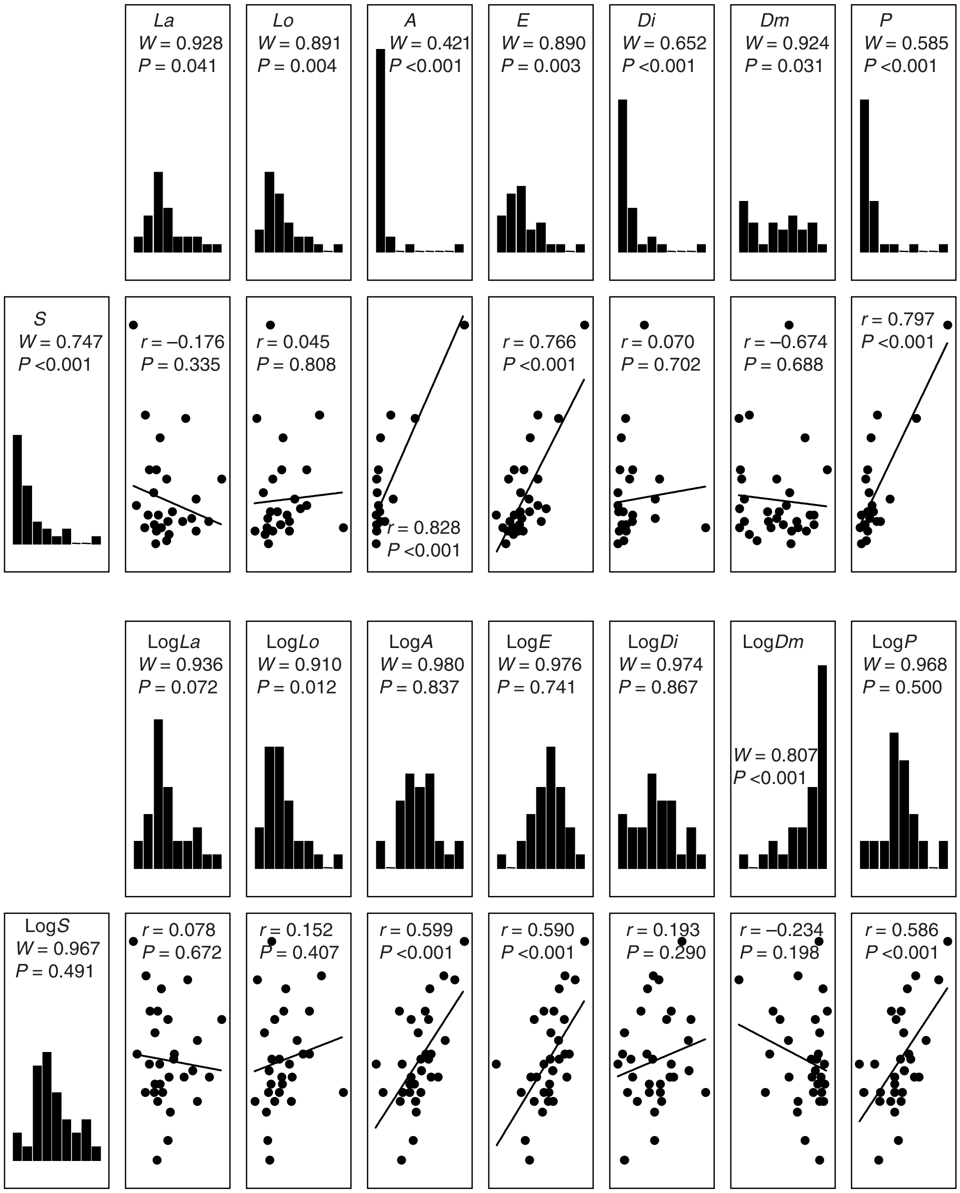

Fig. 3. Normality plot (Shapiro-Wilks *W*-test) of the seven eco-geographical variables and their correlation (Pearson product–moment, *r*) with species richness after and before $\log_{10}$-transformation. *S* = Tenebrionid richness (number of species and subspecies), *A* = area (km^2), *La* = latitude (decimal degrees), *Lo* = longitude (decimal degrees), *E* = elevation (metres above sea level), *Di* = distance to the nearest island (km), *Dm* = distance to the nearest mainland (km), *P* = perimeter (km).

For comparison purposes, I applied other procedures to take into account possible non-linear dependence. I performed both forward and backward stepwise regressions between species richness and the linear, quadratic and cubic terms for the independent variables (see, for example, Lobo and Martín-Piera, 2002; Stefanescu *et al.*, 2004). Here, area, quadratic perimeter and cubic inter-island entered significantly into the model. These results were very similar to those obtained by the aforementioned regressions. Also, both area and quadratic perimeter had low tolerance values (about 0.01) and will be not discussed further.

The importance of island shape in determining species number has received little attention in island biogeography (Simberloff, 1986a; Rydin and Borgegärd, 1988). To test the importance of island shape on species richness, I used some indexes widely applied in landscape ecology (cf. Usher and Keiller, 1998; Farina, 1999):

- perimeter–area ratio: $PARA = P/A$, where P = perimeter and A = area;
- corrected perimeter–area ratio: $CPA = (0.282 * P)/\sqrt{A}$;
- related circumscribing circle: $RCC = (2 * (A/\pi)1/2)$/longest-axis; and
- fractal dimension: $FD = \log P/\log A$.

As for the geographic variables, both a forward stepwise multiple regression and pairwise correlation analysis were used to rank the importance of shape variables in determining species richness.

To assess the impact of multicollinearity on the final results, I checked the values of ‘tolerance’, which largely exceeded the threshold value of 0.1 (Hair *et al.*, 1998).

To study the influence of past (paleogeographic) factors on species richness, Crowell (1986) used island age and sea depth. However, both these measures clearly represent an extremely simplified description of historical island conditions. For this reason, I preferred to use a different approach considering a multidimensional representation of a wider array of paleogeographic descriptors. Unfortunately, the only available map of the whole Aegean area during the Pleistocene is that published by Dermitzakis (1990). Although this map is somewhat outdated, no better paleogeographic map of the area is currently available. On the basis of Dermitzakis’s map, critically evaluated, I considered the following variables to describe the characteristics shown during the Pliocene by each island: (1) connected to the Balkan mainland; (2) connected to the Anatolian mainland; (3) connected to other Cyclades islands; (4) completely isolated; (5) volcanic. Each variable was used as a dummy variable and each island was scored for each variable as 0 (‘no’) or 1 (‘yes’). I used the same variables to describe island conditions during the Pliocene, thus obtaining a total of 10 dummy variables.

These variables were subjected to a factorial analysis using a principal components analysis (PCA) with a VARIMAX normalized rotation using Statistica software (version 4.5, 1993). The four principal-components factors (herein labelled F_p – paleogeographic factors) with an eigenvalue higher than one (77% of total variance) were retained and the loadings examined to determine their relationships with the original variables: F_p1 was mainly connection to the Cyclades in the Pleistocene and connection to the Anatolian mainland in the Pliocene; F_p2 was mainly volcanic activity in both the Pliocene and Pleistocene; F_p3 was mainly connection to the Anatolian mainland in both the Pliocene and Pleistocene; and F_p4 was mainly connection to the Balkan mainland in both the Pliocene and Pleistocene. Thus, F_p1 summarized isolation of islands from other islands, F_p2 their volcanic activity, F_p3 and F_p4 their connection to the mainland areas. To assess if such conditions are responsible for the present variation in species richness, a forward stepwise multiple regression and a pairwise correlation analysis were performed using Statistica software (version 4.5, 1993).

In all aforementioned tests, and in the following ones, statistical significance was set at $P < 0.05$ (all tests were two-tailed). In accordance with the suggestions of Moran (2003), I did not apply the Bonferroni correction.

Identification of island groupings

To assess if the study islands can be arranged into meaningful groups, or if they form a true transitional zone, I applied a fuzzy cluster analysis using the algorithm implemented in the NCSS 97 software. I first constructed a distance matrix using the Jaccard index in SPSS 8.0.0. The Jaccard index is recognized to produce the most valuable results (Shi, 1993) and it is widely used as a measure of beta diversity (e.g. Magurran, 1988; Blondel and Aronson, 1999; MacNally *et al.*, 2004). This dissimilarity matrix was then imported in NCSS to develop the fuzzy analysis.

To choose the appropriate number of clusters, I referred to average silhouette and to Dunn's and Kaufman's partition coefficients. The appropriate number of clusters was that which maximized the average silhouettes, maximizing Dunn's coefficient ($Fc(U)$) and minimizing Kaufman's coefficient ($Dc(U)$). Fuzzy analysis was performed with fuzzifier constant at 2, and with 15 iterations, for a maximum of 16 clusters. On the basis of average silhouettes, the solution with $K = 2$ was considered the best, although on the basis of $Fc(U)$ and $Dc(U)$ coiefficients, solutions with a higher number of clusters could be used (see below).

Dependence of distributional patterns on past and present island characteristics

The Mantel test for correlation of distance data has been sometimes applied to correlate a matrix of biogeographic distance to a matrix of geographic distance (e.g. Sfenthourakis, 1996a; Hausdorf and Hennig, 2005). However, the use of the Mantel test, and that of its derivative partial Mantel test, is controversial (Raufaste and Rousset, 2001; Castellano and Balletto, 2002; Rousset, 2002). Also, it is very difficult to express overall geographic and historical 'similarity' among areas by simply using a dissimilarity coefficient and geographic distances, which inherently requires much compression and distortion of actual multidimensional relationships among areas.

A more appropriate way to assess how island characteristics may have influenced distributional patterns is to quantify the interrelationships between a set of variables that adequately describes various characteristics of the areas and the biogeographic relationships among them. For this purpose, I used canonical correlation analysis (CANCOR). To apply CANCOR, both distributional data (a presence/absence matrix of 32 columns (cases) × 170 rows (variables)) and geographic, shape and paleogeographic parameters (respectively seven, four and ten variables for 32 cases) have to be reduced to a manageable number of variables without substantial loss of information. According to 'rule C' of McGarigal *et al.* (2000), the number of cases (in this study, 32 islands) should be at least three times more than the sum of the two variable sets (thus, the sum should be less than 11). The original presence/absence matrix was then subject to a non-metric multidimensional scaling (MS) using Statistica software (version 4.5, 1993) to obtain a reduced number of dimensions. As a measure of biogeographic similarity among islands, I used the Jaccard coefficient converted to dissimilarity. On the basis of stress values (Shi, 1993), the retention of three dimensions was considered to be sufficiently representative. These three dimensions were used as Y (dependent) variables in CANCOR.

The original geographic, shape and paleogeographic parameters represented an excessively large set of predictors to be used as X (independent) variables in CANCOR. To reduce their number, predictors can be replaced by their principal component scores. Thus, a factorial analysis using PCA was performed with a VARIMAX normalized rotation separately for each set of variables using Statistica software (version 4.5, 1993). For the geographic variables, the three principal components (herein labelled F_g – geographic factors) with an eigenvalue higher than one (85% of total variance) were retained: F_g1 was mainly area, perimeter and elevation; F_g2 was mainly distance to mainland; and F_g3 was mainly longitude. For the island shape parameters, the two principal components (herein labelled F_s – shape factors) with an eigenvalue higher than one (86% of total variance) were retained: F_s1 was the perimeter–area ratio (*PARA*) and fractal dimension (*FD*); and F_s2 was mainly the corrected perimeter–area ratio (*CPA*). Finally, for the paleogeographic variables, the aforementioned four principal paleogeographic factors (labelled F_p1 to F_p4) were considered. These three sets of variables were used as X variables in CANCOR. Thus, the analysis involved 3 Y variables and 9 X variables (3 for geographic, 2 for shape and 4 for paleogeographic parameters respectively), which roughly meets ‘rule C’ of McGarigal *et al.* (2000). In addition to this overall CANCOR, I also performed three separate CANCORs to thoroughly elucidate the relationships between the biogeographic relationships among islands and the three sets of island characteristics (geography, shape and paleogeography) separately. CANCORs were performed using NCSS 97 software.

RESULTS

Effect of island size and habitat diversity

Using number of habitats as a measure of habitat diversity, the multiple regression model selected is: $S = -10.020 + 0.821 \log A + 6.986\ NH$ ($R^2 = 0.599$, $P < 0.00001$). The results of path analysis are shown in Fig. 2. The area effect on species (indirect) is $a_1b_1 = 0.298$. Thus, the area effect on species (total) $= b_2 + a_1b_1 = 0.641$, while the habitat effect on species (total) = direct effect (b_1) = 0.526. The magnitude of the two area effects – direct and indirect – on species per island is roughly equal ($0.343 \approx 0.298$). By contrast, the direct effect of habitat number on species richness exceeds the direct area effect on species ($0.526 > 0.343$), but the total effect of area, when direct and indirect effects are summed, is greater than the effect of habitat number ($0.641 > 0.526$). If elevation is used as a measure of habitat diversity, the model applied is: $\log S = -0.121 + 8.007 * 10^{-5}\ A + 0.414 \log E$ ($R^2 = 0.461$, $P < 0.001$). The path coefficients are:

- effect of area on elevation (direct) = $a_1 = 0.568$
- effect of habitat number on species (direct) = $b_1 = 0.357$
- effect of area on species (direct) = $b_2 = 0.410$
- effect of area on species (indirect) = $a_1b_1 = 0.203$

The effect coefficients are:

- effect of area on species (total) = direct (b_2) + indirect (a_1b_1) = 0.613
- effect of habitat on species (total) = direct effect (b_1) = 0.357

The magnitude of the direct effect of area on species per island is greater than the indirect effect ($0.410 > 0.203$). Similarly, the direct effect of habitat number on species richness was inferior to the direct area effect on species ($0.357 < 0.410$), and the total effect of area, when direct and indirect effects are summed, is nearly twice the effect of habitat number ($0.613 > 0.357$).

Overall, path analysis shows that island area contributes to species number both directly and indirectly, through habitat diversity. While the direct effects of area may be inferior or superior to the direct effect of habitat diversity, depending on the measure of habitat diversity used, the total effect of area is greater than the effect of habitat diversity. However, area exerts about half its overall effect on species number through a powerful effect on habitat number, and a substantial proportion through a powerful effect on elevation. This result clearly shows the importance of habitat diversity in determining gamma diversity.

Variations in species richness

The results of stepwise regression analysis between tenebrionid richness and geographical variables are given in Table 2. Only area showed a statistically significant (positive) regression coefficient. Use of untransformed values of species richness gave similar outcomes, with the exception that log-latitude gave a significantly negative contribution. In all cases, no distance effect was detected.

The stepwise regression points to the importance of area for species richness, but it is unsatisfactory as an explanation of the mechanisms involved because of the close relationship between area and habitat diversity, especially if measured as elevation ($r_s = 0.844$, $P < 0.000001$).

Shape *per se* has little effect on species richness. For multiple regression using log$S$, both the related circumscribing circle (*RCC*) and the perimeter–area ratio (*PARA*) entered the model, but the contribution of these variables, as well as the total model, were not significant (Table 2). By contrast, using S, *RCC* gave a slightly negative significant contribution to the model. Thus, the effect that shape has on species richness (if any) is such that long thin

Table 2. Results of stepwise regression analyses between tenebrionid richness (log-transformed) and geographical and shape variables

	β	SE of β	B	SE of B	P
Geographic variables					
Intercept			10.619	5.239	0.052
Log*A*	0.648	0.147	0.280	0.064	0.000
Log*La*	−0.292	0.151	−6.512	3.365	0.063
Log*Di*	0.163	0.148	0.105	0.095	0.278
Shape variables					
Intercept			1.668	0.265	<0.00001
RCC	−0.317	0.170	−0.811	0.434	0.072
PARA	−0.298	0.170	−0.115	0.065	0.090

Note: A = area (km^2), La = latitude (decimal degrees), Di = distance to the nearest island (km), $PARA$ = perimeter–area ratio, RCC = related circumscribing circle, β = standardized regression coefficient (weight), B = non-standardized regression coefficient, SE = standard error. Regression results for geographic variables: $R = 0.665$, $R^2 = 0.442$, $Ra^2 = 0.383$; $F_{3,28} = 7.403$, $P < 0.001$, standard error of the estimate = 0.239. Regression results for shape variables: $R = 0.414$, $R^2 = 0.172$, $Ra^2 = 0.115$; $F_{2,29} = 3.004$, $P = 0.065$, standard error of the estimate = 0.287.

islands have more species than more rounded ones. Pairwise correlations produced similar results (Fig. 3).

Therefore, distance effects were small in multiple regressions and not appreciable in pairwise correlations. Thus it appears unreliable that present colonization processes may play a substantial role in determining gamma diversity. Island shape did not substantially influence species richness. In particular, in contrast with the idea that round shape is preferable for refuges, Aegean tenebrionid richness appears to be increased slightly by an elongated island shape.

Pairwise correlation revealed no correlation between richness (both transformed and untransformed) and F_p1 to F_p4. Stepwise multiple regression using untransformed richness gave a non-significant model, where only F_p1 entered the equation without a significant contribution. No variable entered the model if log-transformed values of richness were used. Thus paleogeography does not appear to significantly influence present gamma diversity, which is mainly affected by area size and habitat diversity.

Identification of island groupings

As expected for a transitional area, the tenebrionid fauna of the Aegean Islands shows an extremely high degree of fuzziness. Dunn's coefficients ($Fc(U)$) were constantly rather low, while Kaufman's coefficients ($Dc(U)$) were constantly high. The highest average silhouette value was low (0.09), and many values were negative.

The best values of $Fc(U)$ and $Dc(U)$ were recorded for negative or very low values of average silhouette and for a very high number of clusters, which contrast with the scope of finding a reasonable number of island groupings. Thus I selected the solution with two clusters, which maximizes silhouette values.

To obtain meaningful groups, silhouette values should be positive and most of them should be greater than 0.50. The fact that none of the rows in this analysis was greater than 0.50 and that the 'Anatolian cluster' contained non-Anatolian islands with negative silhouette values (Table 3), clearly demonstrates the transitional character of the area, which makes it difficult to subdivide islands into meaningful, well-separated clusters.

Dependence of distributional patterns on past and present island characteristics

With all canonical roots together – that is, without any roots removed – the overall CANCOR analysis gave $\chi^2_{27} = 55.384$, $P = 0.00103$ (canonical $R^2 = 0.697$). For the second root, $\chi^2_{16} = 26.111$, $P = 0.053$ (canonical $R^2 = 0.504$). Thus, only the first root should be considered. However, as the second root is 'nearly' significant, I considered it more conservative to examine this root too. Finally, the third root was clearly not significant (canonical $R^2 = 0.306$, $\chi^2_7 = 8.945$, $P = 0.257$).

The total variance extracted in the X set (36.517%) is mainly represented by the variance extracted by the first and second roots, while redundancy highlights the importance of the first root (see Table 4). The total redundancy for the Y set was 50.228%. Looking at the factor structure (structure coefficients or canonical loadings), the first dimension extracted by multidimensional scaling (MDS) was mainly influenced by F_p3 and F_g3, while the second dimension was influenced by F_g1. The third dimension of MDS is represented by root 3, which however is not significant. This root appears mainly influenced by F_p4. Thus, both connection to the Anatolian mainland in both the Pliocene and Pleistocene (represented by F_p3) and longitude (represented by F_g3) appear to be mainly

Table 3. Identification of island groupings by fuzzy analysis

Islands	Cluster	Silhouette amount
Amorgos	1	0.1891
Anafi	1	0.0664
Andros	1	0.1141
Castellorizon	2	0.0636
Chios	2	0.1088
Euboea	2	−0.0160
Folegandros	1	0.1517
Ios	1	0.2195
Karpathos	2	0.0946
Kea	2	−0.0278
Kimolos	1	0.1091
Kithnos	1	0.1091
Kos	2	0.0612
Kriti	2	0.0189
Lemnos	2	0.0112
Lesvos	2	0.0202
Mikonos	1	0.1752
Milos	1	0.1470
Naxos	1	0.0736
Pano Koufonissi	1	0.2145
Paros	1	0.1470
Rhodos	2	0.0827
Samos	2	0.0289
Santorin	1	0.0937
Serifos	2	−0.0616
Sifnos	1	0.1928
Sikinos	1	0.1685
Siros	1	0.1107
Skiros	1	0.1010
Skopelos	2	−0.0422
Thasos	2	0.0006
Tinos	1	0.1245

Note: Identified clusters: 1 = Balkan cluster, 2 = Anatolian cluster.

responsible for the biogeographic relationships among islands represented by the first axis of the MDS. A combination of area, perimeter and elevation (summarized by F_g1) is responsible for the biogeographic relationships among islands represented by the second axis of the MDS.

Considering only the geographic variables, with all canonical roots together, $\chi^2_9 = 38.934$, $P < 0.00001$ (canonical $R^2 = 0.641$). For the second root, $\chi^2_4 = 10.735$, $P = 0.030$ (canonical $R^2 = 0.323$). For the third root, $\chi^2_1 = 0.027$, $P = 0.869$ (canonical $R^2 = 0.001$). Thus, the first two roots should be considered. The total variance extracted in the X set (100%) is actually equally composed of the variance extracted by the three roots, but redundancy is highest for root 1. The total redundancy for the Y set was 32.162%. Looking at the factor structure, the

Table 4. Results from CANCOR with all canonical roots analysed

	Factor structure		
	Root 1	Root 2	Root 3
Distributional patterns (coordinates from MDS)			
Dimension 1	0.930	−0.267	−0.250
Dimension 2	0.179	0.928	−0.326
Dimension 3	0.319	0.259	0.912
Variance extracted	0.333	0.333	0.333
Redundancy	0.232	0.168	0.102
Geographic and shape characteristics (loadings from PCA)			
Geographic dimension 1	−0.328	0.752	0.169
Geographic dimension 2	−0.507	−0.142	0.064
Geographic dimension 3	0.728	0.224	−0.191
Shape dimension 1	0.210	−0.248	−0.274
Shape dimension 2	0.068	−0.005	−0.012
Paleogeographic dimension 1	0.382	−0.338	0.353
Paleogeographic dimension 2	−0.039	0.317	−0.283
Paleogeographic dimension 3	0.776	0.281	0.070
Paleogeographic dimension 4	−0.080	−0.036	−0.492
Variance extracted	0.189	0.110	0.066
Redundancy	0.132	0.056	0.020
Eigenvalues	0.697	0.504	0.306

Note: MDS = multidimensional scaling.

first dimension extracted by MDS (root 1) was mostly influenced by F_g3 and the second dimension (root 2) by F_g1. In this case, the influence of area, perimeter and elevation (summarized by F_g1) is significant.

Considering only the paleogeographic variables, $\chi^2_{12} = 29.650$, $P < 0.003$ (canonical $R^2 = 0.558$). For the second root, $\chi^2_6 = 7.604$, $P = 0.269$ (canonical $R^2 = 0.207$). Thus, only the first root should be considered. The total variance extracted in the X set (75%) is equally represented by the variance extracted by the three roots, but redundancy is highest for root 1. The total redundancy for the Y set was 27.117%. Looking at the factor structure, the first dimension extracted by MDS was mostly influenced by F_p3.

Finally, a CANCOR applied to the shape parameters alone did not produce significant results ($\chi^2_6 = 2.571$, $P = 0.861$, canonical $R^2 = 0.086$).

On the whole, longitude (represented by F_g3) and past connection to Anatolia (F_p3) appear to be mainly responsible for the biogeographic relationships among islands represented by the first axis of the MDS. A combination of area, perimeter and elevation (summarized by F_g1) is responsible for the biogeographic relationships among islands represented by the second axis of the MDS, which appears to have a minor biogeographic significance. Finally, island shape did not correlate with any MDS axis.

Thus, longitude appears to be the geographic variable that mostly affects biogeographic relationships among islands (beta diversity), whereas past connection with Anatolia is the most important paleogeographic factor. These two factors are interrelated, because islands with higher longitude are those nearest to Anatolia and were therefore connected to this mainland. The first axis of MDS seems to be a strictly (paleo)geographic space in the biogeographic relationships, dominated by the influence of the Anatolian fauna in determining present distribution patterns. Obviously, one cannot exclude that the influence of longitude on biogeographic similarity among islands reflects present immigration from the two opposite mainland areas (the Balkans and Anatolia). However, as longitude and paleogeographic connection to Anatolia (a strictly historical factor) appear to interact in a similar fashion, this result suggests that the correlation between biogeographic patterns and longitude may be, at least partly, a reflection of historical conditions.

Other geographic variables, such as area, elevation and perimeter, have a secondary role. Area, perimeter and elevation may be regarded as parameters more or less related to habitat diversity. These variables are related to the second MDS axis, which thus can be considered an expression of a more strictly ecological space. Therefore, the ecological space appears to have a secondary role in determining biogeographic relationships among islands. Finally, island shape has a completely negligible effect on distributional patterns.

DISCUSSION

In this study, neither distance to the mainland nor distance to the nearest island was found to be of any statistical importance in affecting tenebrionid richness. Thus, the present patterns of tenebrionid gamma diversity cannot be explained by present immigration from the mainland or by inter-island (stepping stone) colonization. In contrast, the Aegean tenebrionids appear to be a relict fauna (cf. Hausdorf and Hennig, 2005), as found for other very sedentary animals such as the land snails (Welter-Schultes and Williams, 1999). The positive dependence of gamma diversity on island area size and habitat diversity is a consequence of the fact that larger and/or more diversified islands could have retained more species after saturation.

Some authors have tried to derive some recommendations about refuge shape from island biogeography theory, suggesting that round refuges are preferable. However, the importance of island shape on species number has rarely been addressed (Simberloff, 1986a). As a general rule, island shape does not appear to have any substantial role in determining species richness (cf. Faeth and Kane, 1978; Blouin and Connor, 1985; Rydin and Borgegärd, 1988). If anything, available data indicate that there is a slight tendency for elongated islands to have more species than rounded ones. Aegean tenebrionid gamma diversity is enhanced on elongated islands. This parallels Simberloff's (1986a) findings for the bird richness on the Cyclades. For the Aegean tenebrionids, this unexpected result may be related to the fact that the most elongated islands are in some cases the largest ones (e.g. Kriti, Euboea, Rhodos), or those that have retained more species because of higher habitat diversity, or which experienced a longer evolutionary process (e.g. Kriti).

Most previous studies have considered habitat diversity and area together as potential determinants of diversity, but few have considered their simultaneous effects on species number (Kohn and Walsh, 1994; Ricklefs and Lovette, 1999). In the present study, I attempted to determine the form of relation between species number, habitat diversity and area for Aegean tenebrionids. It is difficult to distinguish the effect of area *per se* and habitat diversity when these variables are interrelated (cf. Deshaye and Morisset, 1988; Rydin and Borgegärd, 1988; Torres and Snelling, 1997; Ricklefs and Lovette, 1999; Davidar *et al.*, 2001; Magura *et al.*, 2001). Welter-Schultes and Williams (1999) interpreted a positive influence of elevation (coupled with area) on the Aegean land snail species as a consequence of the greater range of potential habitats associated with higher island elevation. This interpretation is tenable for tenebrionids. Path analysis distinguished the effect of island size on species per island from the direct effect of habitat diversity, using habitat diversity both as an explanatory variable for species and as a response variable for area. Habitat diversity can increase species number on larger islands in various ways (e.g. by the addition of habitats and increasing extent of habitat types) that are difficult to distinguish (Kohn and Walsh, 1994).

Ricklefs and Lovette (1999) suggested that different taxa differ in their responses to area and habitat diversity according to their biological traits. Strong habitat-diversity effects are likely in taxa with: (1) high vagility (because between-island movements could lead to the rescue of populations on the verge of extinction, reducing the effect of area alone on species richness); (2) high degrees of habitat specialization (making species richness more sensitive to habitat diversity and perhaps less sensitive to area *per se*); (3) life cycles that include a resistant resting stage that reduces vulnerability to catastrophic extinction (and thereby reduces the influence of island area on species richness); or a combination of these traits.

The Aegean tenebrionids have low vagility, as shown by the lack of influence of island distance on species richness, a result of the prevalence of apterous species. Aptery in Aegean tenebrionids evolved before island colonization, and it is not a consequence of living on islands. Although little is known about the ability of tenebrionids to survive or remain afloat in salt water, several lines of evidence suggest that the probability that wingless tenebrionids colonize islands by sea dispersal is negligible (Palmer, 1998; Finston and Peck, 1995). As to possible habitat specialization, it is usually low in tenebrionids (cf. Ayal and Merkl, 1994; Krasnov and Shenbrot, 1997; Carpaneto and Fattorini, 2001). Thus, none of the hypotheses presented by Ricklefs and Lovette (1999), which appear more relevant to equilibrial faunas, appears to clearly operate in the Aegean tenebrionids, which are a relict fauna.

From a relict perspective, one can suppose that different islands were reached by immigrants in past times, and that they retained more or fewer species according to their area and habitat diversity. This appears to be the case of the Aegean tenebrionids. On the one hand, since distance does not negatively affect present colonization processes, the equilibrium models should be rejected, and a relict model should be accepted. On the other hand, a habitat diversity model could be evoked to explain the positive species–area relationship. After saturation, large islands retained more species because they retained greater habitat diversity. Finally, an effect of area *per se* could also contribute: larger islands retained more species because harbouring larger populations was less affected by extinction.

To summarize, we postulate that: (1) islands were colonized during Pleistocene falls in sea level, while present immigration is negligible (allowing for the lack of distance effects); (2) after Pleistocene saturation, islands retained more or fewer species according to their size, both as an effect of area *per se* (lower extinction in larger populations) and habitat diversity (larger areas have more and/or larger habitats, allowing for the presence of species with different ecological needs). Pleistocene islands characteristics, however, did not influence tenebrionid gamma diversity (species richness). It is in fact extremely difficult to obtain accurate measures of island distance to the mainland in the Plio-Pleistocene. Moreover, as most islands were connected to one another, in many cases such measures cannot be applied. Finally, many islands were directly connected to the adjacent mainlands. Thus, they formed a rather homogeneous system in terms of area and ease of colonization. If islands were 'identical' with respect to the number of species they could have hosted, this does not mean that they were identical in terms of the 'kind' of species they hosted and retained. As discussed above, the number of species retained was possibly regulated by area size and habitat diversity. It is an extremely difficult task to establish how habitat diversity could have operated in the Plio-Pleistocene. Thus, we cannot formulate any hypothesis about the role of habitat in moulding the faunas established on the islands in the Plio-Pleistocene. However, we can correlate some island characteristics in the Plio-Pleistocene with the biogeographic characteristics of the species. For example, we can suppose that islands close (or connected) to the Balkan coasts were mainly colonized by Balkan species, whereas islands close (or connected) to the Anatolian coasts were mainly colonized by Anatolian species.

Identification of island groupings by fuzzy analysis supports this model, although the extremely complicated paleogeography of the area makes it difficult to establish clearly defined island clusters. Fuzzy analysis supports the existence of faunal regions defined by Pleistocene island configurations. In particular, a faunal discontinuity between the western and central Aegean Islands on one side, and the islands close to the Anatolian coast on the other side, as determined by fuzzy groupings, is consistent with the persistence (from the Messinian to the Pleistocene) of a sea barrier between these two groups of islands. A separate position of Kriti (associated with the Anatolian cluster, but with a positive silhouette value, in contrast with the negative values exhibited by all other islands) also supports its different biogeographic position.

Obviously, finding that islands close to the Anatolian coasts are grouped together does not necessarily imply they were reached by such species during the Plio-Pleistocene, because this pattern could also result from present immigration. However, we observed no influence of present distance on tenebrionid species numbers, thus suggesting that present immigration is negligible for these insects. More importantly, correlations between present distribution patterns and island geography, shape and paleogeography revealed that the composition of island faunas is more dependent on past conditions than on present ones. Both connection to the Anatolian mainland in the Plio-Pleistocene and longitude appeared to be mainly responsible for the biogeographic relationships among islands (beta diversity). These two factors are however interrelated, because islands with lower longitude are those closest to Anatolia and were therefore connected to this mainland, and a possible present effect of longitude cannot be separated from its effect in the past. Thus, present tenebrionid beta diversity appears to be dominated by paleogeographic factors. Although longitude did not change appreciably in the Pleistocene, in the past 10 million years the southern parts of the Aegean were stretched over 400 km southwards, while the north remained locked (Kissel and Laj, 1988). The mainland between Albania and Peloponnisos underwent a clockwise rotation of 50°, and the NW Aegean one of 30–40°, since the Middle Miocene (Van Hinsbergen *et al.*, 2005). While Kriti has not rotated since 10 Ma, Karpathos and Rhodos have experienced a counterclockwise rotation (Duermeijer *et al.*, 2000). When the Aegean landmass was stretched in this north–south direction and islands were rotated, the ranges of strictly resident animals like tenebrionids would be expected to become stretched together with the land on which they lived. Such processes could have contributed to enhanced species richness at lower latitude and possibly played a role in determining a positive influence of longitude on beta diversity. However, the aforementioned geodynamic processes occurred mainly before the probable radiation of most of the species. Thus, such processes may have played an important role in moulding the ranges of some ancestors, but are very hard to detect in the present fauna, likely more affected by the Pleistocene conditions.

Some evolutionary considerations may support this view. First, islands close to each other tend to harbour different endemic subspecies of the same tenebrionid species, or morphologically strictly related species (Koch, 1948; Fattorini *et al.*, 1999; Chatzimanolis *et al.*, 2002). According to Fattorini (2002a), these species/subspecies endemic to individual islands or groups of strictly related islands originated allopatrically, when former Pleistocene island groupings were fragmented by the restored sea level. The phylogenetic work of Chatzimanolis *et al.* (2002) on the specious genus *Dendarus* confirmed this model. Another important line of evidence (usually neglected in biogeographic research) is the absence on the islands of certain species, which are in contrast common on the adjacent mainland areas. The striking, large-sized, euryoeceous genus *Gnaptor*, which is abundant and widely distributed over the entire Balkan area to Anatolia, is completely absent from the Aegean Islands. This absence on the Aegean Islands suggests that the genus evolved or reached its present distribution after Pleistocene island connections, when the islands were isolated and not more colonizable. Similarly, the well-characterized genus *Enoplopus* includes two species: *E. reitteri* (distributed in Greece, including the Peloponnese) and *E. velikensis* (widely distributed in Southern Europe), both absent from the Aegean Islands. *Helops coeruleus* and *Stenomax aeneus* are two striking species, both widely distributed in Greece (and possibly occurring in Anatolia), but absent from the islands (with the exception of *H. coeruleus* on Euboea, an island that is however contiguous with mainland Greece). *Nalssus plebejus* is distributed in both mainland Greece and Anatolia but occurs, on the Aegean Islands, only on those currently close to the Balkan coasts (Euboea and Thasos). These distribution patterns are paralleled by other tenebrionid species. They make unrealistic the alternative hypothesis that the Aegean area could have acted as a relevant centre of radiation, that most species evolved before 9 Ma and that, later, after land-bridges appeared, they invaded the mainlands. An island colonization from mainland populations during the Pleistocene appears more realistic. Obviously, after colonization, when Pleistocene island groupings were fragmented into the present separate islands, populations were subdivided, allopatrically evolving as different, strictly related, species or subspecies.

On the whole, past inter-island connections, and island connections to the mainland, appear to be predominantly responsible for present patterns of species distribution (beta diversity), while area *per se* and habitat diversity are mainly responsible for variations in species richness among islands (gamma diversity).

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