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Faunal patterns in tenebrionids (Coleoptera: Tenebrionidae) on the Tuscan Islands: The dominance of paleogeography over Recent geography

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Abstract. The tenebrionid fauna of the Tuscan Islands (Central Italy) is well known and is an ideal system for studying the role of current and historical factors in determining the biogeographical patterns in a complex archipelago. Cluster analyses, species-area relationships and Mantel tests were used to investigate the influence of current geography and Pleistocene connections with the mainland on the structure of insular communities. Current biogeographical similarity patterns fit both Pleistocene and Recent geography, but marked effects of Pleistocene geography appeared when the influence of Recent geography was removed. Thus, in contrast to more mobile insects, such as butterflies and chrysidids, tenebrionid colonization is likely to have occurred via land-bridges when the islands were connected to the mainland in the Pleistocene. The relict distributions of organisms with poor mobility should be of great concern to conservationists, because depletion of island populations cannot be balanced by new immigrations from mainland populations. The continued influence of man on the Tuscan Islands has adversely affected the natural environment, however, man made habitats may also be colonized and exploited by tenebrionids.

INTRODUCTION

Islands can be roughly classified into two main categories: "landbridge islands" and "oceanic islands" (MacArthur, 1972; Whittaker, 1998). Landbridge islands are those that were recently connected to the mainland, or resulted from the fragmentation of larger landmasses: thus the current biota did not have to cross sea barriers. By contrast, oceanic islands emerged spontaneously as individual islands and have never been connected to the mainland, thus, their colonists must have crossed a water gap. The equilibrium theory proposed by MacArthur & Wilson (1967) stimulated interest in oceanic islands and recently a general model was proposed that takes into account island evolution through time (Whittaker et al., 2008; Fattorini, 2009b). In contrast, landbridge islands have attracted less attention and there is no comprehensive theory on the evolution of their biotas, although it is likely that the poorly mobile species in their faunas and floras contain relict species that underwent a relaxation process (Fattorini, 2002b, 2007b, 2008b, c, 2009a).

The Mediterranean Basin includes a large number of landbridge islands, which were connected to the mainland or adjacent larger islands during the last glaciation (e.g., most of the Aegean, Dalmatian and small islands around Corsica and Sardinia), or which originated from the fragmentation of previous mainland areas (the Balearic Islands, Corsica, Sardinia and Cyprus). There are few typical oceanic islands in the Mediterranean: examples are some volcanic islands in the Aegean Sea and several islands off Sicily.

The Tuscan Archipelago, a group of small islands in the Tyrrhenian Sea (West Mediterranean), includes islands of both kinds, because some islands were connected to the mainland during Pleistocene regressions and others were not. Furthermore, because they are located between the Corsardinian plate (Corsica plus Sardinia) and Tuscany region (Central Italy), the expectation is that the fauna of the Tuscan Islands is transitional. Thus, this small archipelago is particularly complex from a biogeographical point of view.

The biogeography of the Tuscan Archipelago has been studied over a long period and the major ecological and historical factors that are potentially responsible for present day distributional patterns have been highlighted, making this archipelago one of the best investigated in the Mediterranean Basin (e.g., Baroni Urbani, 1971; Società Italiana di Biogeografia, 1974; Mariotti, 1990; Piantelli et al., 1990; Dapporto & Cini, 2007; Dapporto & Strumia, 2008; Dapporto et al., 2007; Fattorini, 2009a).

The consensus is that paleogeography is a key factor in determining the distribution of plants and animals on this archipelago (see references in Mariotti, 1990 and in Dapporto & Cini, 2007). According to this view, islands which were connected to Tuscany during Pleistocene glacial maxima are characterized by a preponderance of species that reached the Tuscan Islands from the Italian mainland, whereas islands closer to Corsardinia, but which remained isolated during Pleistocene glacial maxima, exhibit a larger proportion of species present in Corsica and/or Sardinia but absent from Tuscany. In fact, recent studies indicate that, at least for highly mobile animals such as chrysidids and butterflies, the transitional pattern can be simply explained by current geography alone (Dapporto & Cini, 2007; Dapporto & Strumia, 2008), thus supporting a model similar to that proposed for oceanic islands, although even for the current butterfly fauna there is some indication of a Pleistocene effect (Fattorini, 2009a).

According to the model postulated by Fattorini (2009a), landbridge islands of the Tuscan Archipelago were largely colonized (and possibly saturated) by different animal groups during the Pleistocene sea regressions, followed by extinctions as a result of area and hence habitat loss. However, mobile animals can currently colonize islands and erase the historical signal, thus determining a negative correlation between species richness and distance from the nearest land mass as is observed for oceanic islands. By contrast, even small distances preclude regular colonization of islands by less mobile groups, so that there is no correlation between species richness and distance for these animals. Thus, the role of dispersal should be taken into account when studying the evolution of the faunas of archipelagos that include landbridge islands.

Tenebrionid beetles typically have poor powers of dispersal and are thus excellent organisms for studies on the biogeography of a paleogeographically varied archipelago. They are a highly diversified group in Mediterranean coastal areas and a conspicuous component of the beetle fauna in terms of species richness, abundance and biomass, being particularly species-rich even on islands (Fattorini, 2008c). Because of their size small islands consist mainly of coastal ecosystems, which are under severe threat (Morey & Martínez-Taberner, 2000). Although montane tenebrionid species occur on very large islands, such as Sardinia, Corsica, Sicily, Crete, Euboea and Cyprus, where there are high altitude biotopes, most of the tenebrionid species inhabiting small islands are exclusively or prevalently associated with meadows, Mediterranean maquis or beach-dune ecosystems (Fattorini, 2002a, 2008a, c; Fattorini & Fowles, 2005). Thus, tenebrionids are an important insect group in these severely threatened ecosystems. Also, small islands host unique assortments of species, sometimes including endemic taxa (Fattorini, 2006d, 2007a, 2008c), usually represented by small populations that are vulnerable to extinction (Fattorini, 2008a, b).

Most of the tenebrionids inhabiting the Tuscan Islands are flightless. These flightless species also occur in the adjacent source areas (i.e., Corsardinia and Tuscany) or, if endemic, belong to flightless genera. Therefore, flightlessness in these insects evolved before island colonization, and it is not a consequence of living on islands. Although flightlessness greatly reduces the beetles' ability to cross water barriers, other dispersal mechanisms, like rafting and water transport, may enable flightless tenebrionids to colonize oceanic islands (cf. Fattorini, 2002b). Therefore, the tenebrionids of the Tuscan Islands may be an excellent model group for studying the role of current and historical factors in determining the biogeographical patterns on an archipelago, which includes both landbridge and oceanic islands.

The tenebrionids of the Tuscan Islands have been investigated by naturalists for more than a century and all of the major islands of this archipelago are well known faunistically (cf. Gardini, 1976, 1979; Leo, 1998; Fattorini & Leo, 2000; Lo Cascio et al., 2000). However, there is no detailed study of the role of current and historical factors responsible for determining the biogeographical patterns. An analysis of the relative importance of current and historical factors is particularly urgent because of the concern over the conservation of the faunas of these islands. The recent development of conservation biogeography (Whittaker et al., 2005) stresses the importance of considering biogeographical information when assessing conservation priorities. Thus, understanding the processes underlying the biogeographical patterns of tenebrionids on the Tuscan Islands may serve as a case study for addressing some general problems of biological conservation of relatively sedentary animals on landbridge archipelagos.

The aims of this paper were to: (1) investigate the biogeographical relationships of the tenebrionid faunas of the Tuscan Islands; (2) determine the relative importance of current (Recent) and historical (Pleistocene) geography in determining such patterns; (3) assess the mechanisms that may explain the role of Recent and Pleistocene factors; and (4) discuss some of the implications for biodiversity conservation.

MATERIAL AND METHODS

Data sources

The islands studied included: Capraia, Gorgona, Montecristo, Elba, Pianosa, Giglio, Giannutri and the fossil-island of Mt Argentario (Dapporto & Cini, 2007).

A total of 65 taxa, 13 of which (20%) are endemic, are known from these islands (Table 1). There are indications that various insular populations of tenebrionid beetles described as subspecies differ profoundly genetically (cf. Chatzimanolis et al., 2003; Ferrer, 2008). The current taxonomic dividing line between species and subspecies, as applied to the tenebrionids of the Tuscan Islands, is arguably arbitrary, and the exclusion of subspecies could result in a significant underestimate of endemic island tenebrionid diversity (cf. Lewis et al., 1998; Fattorini, 2007a). This is particularly the case for several allopatric populations of the genera *Asida* and *Opatrum* endemic to the Tuscan Archipelago. Thus, I considered both species and subspecies as "evolutionarily significant units" (Ryder, 1986; Samways, 1998) and include both categories in all analyses. For this the "phylogenetic species concept" (Isaac & Purvis, 2004) is used as the smallest diagnosable and/or monophyletic biological entity. The validity of the endemic *Asida luigionii insularis* is disputed and this taxon has been considered only in the analyses regarding endemic taxa.

To avoid the risk of including species introduced by man I have excluded from all analyses cosmopolitan species strictly associated with human food, such as *Palorus subdepressus*, *Gnatocerus cornutus*, *Alphitobius diaperinus* and of the genera *Tenebrio* and *Tribolium*. The native occurrence of the anthropophilous species of the genus *Blaps* is doubtful. Although these species are native to the Mediterranean area their occurrence on individual islands may be a result of a recent introduction. Thus, a second set of analyses were done excluding these doubtfully native species.

Finally, analyses omitting widely distributed (W) species (i.e., species occurring in both Corsardinia and Tuscany, as well as on the Tuscan Archipelago) were done on only the Sardo-Corsican (SC) species (i.e., species occurring in both Corsardinia and on the Tuscan Archipelago, but not in Tuscany) and Tuscan (T) species (i.e., species occurring in both Tuscany and

Table 1. Distribution of tenebrionid beetles on the Tuscan Islands. Although unnamed, Montecristo's population of *Opatrum sculpturatum* is considered to be different from other populations (cf. Gardini, 1976). Distribution: C – Corsardinian taxon, E – taxon endemic to Tuscan Islands, T – Tuscan taxon, W – widespread taxon. Nomenclature follows Löbl & Smetana (2008).

	Distribution	Gorgona	Capraia	Elba	Pianosa	Giglio	Montecristo	Giannutri	Mt Argentario
Tentyria italica Solier, 1835	T	0	0	1	0	1	0	0	1
Stenosis sardoa sardoa (Küster, 1848)	C	0	1	1	0	0	0	0	0
Stenosis sardoa ardoini Canzoneri, 1970	W	0	0	1	1	1	0	0	1
Stenosis brenthoides brenthoides (Rossi, 1790)	T	1	0	1	1	0	0	0	1
Stenosis angusticollis anugusticollis (Reiche, 1861)	W	0	0	1	0	1	1	0	0
Stenosis intermedia intermedia (Solier, 1838)	T	1	0	1	1	0	0	0	0
Dichillus minutus (Solier, 1838)	T	0	1	0	0	0	0	0	1
Dichillus corsicus (Solier, 1838) complex	C	0	1	1	0	1	1	0	0
Asida sabulosa sabulosa (Fuessly, 1775)	T	0	0	0	0	0	0	0	1
Asida luigionii luigionii Leoni, 1910	T	0	0	1	1	0	1	1	1
Asida luigionii doriae Leoni, 1910	E	0	0	0	0	1	0	0	0
Asida gestroi gestroi Leoni, 1910	E	0	0	0	0	0	1	0	0
Asida gestroi tyrrhena Leoni, 1910	E	1	0	0	0	0	0	0	0
Asida gestroi capraiensis Gridelli, 1972	E	0	1	0	0	0	0	0	0
Asida gestroi gardinii Lo Cascio, 2000	E	0	0	0	1	0	0	0	0
Asida longicollis Solier, 1836	C	0	1	0	0	0	0	0	0
Akis bacarozzo (Schrank, 1786)	W	0	1	1	1	0	0	0	1
Scaurus striatus Fabricius, 1792	W	0	1	1	1	1	0	0	1
Pimelia bipunctata papii Canzoneri, 1963	T	0	0	1	1	0	0	0	0
Blaps gigas (Linné, 1767)	W	0	1	0	1	1	0	0	0
Blaps gibba Laporte de Castelnau, 1840	W	0	1	1	1	1	0	0	0
Blaps lethifera lethifera Marsham, 1802	W	0	1	1	0	0	0	0	0
Blaps mucronata Latreille, 1804	W	0	0	1	1	1	0	0	0
Dendarus coarcticollis (Mulsant, 1854)	W	1	1	1	1	1	1	1	0
Dendarus lugens (Mulsant & Rey, 1854)	T	0	0	1	1	1	0	1	0
Phylan abbreviatus italicus (Reitter, 1904)	T	0	0	1	0	0	0	0	0
Pedinus meridianus Mulsant & Rey, 1853	W	1	1	1	1	1	0	1	1
Colpotus strigosus strigosus (Costa, 1847)	T	0	0	1	0	0	0	0	0
Colpotus strigosus oglasensis Gardini, 1976	E	0	0	0	0	0	1	0	0
Allophylax picipes picipes (Olivier, 1811)	W	0	0	0	0	0	0	0	1
Gonocephalum granulatum nigrum (Küster, 1849)	W	0	0	1	0	0	0	0	0
Gonocephalum assimile (Küster, 1849)	W	0	0	0	0	0	0	1	0
Gonocephalum obscurum obscurum (Küster, 1849)	W	0	1	1	0	0	0	0	0
Gonocephalum rusticum (Olivier, 1811)	W	1	1	1	1	0	0	0	0
Opatrum sculpturatum ilvense Razzauti, 1919	E	0	0	1	0	0	0	1	1
Opatrum sculpturatum igiliense Razzauti, 1919	E	0	0	0	0	1	0	0	0
Opatrum sculpturatum ssp.?	E	0	0	0	0	0	1	0	0
Opatrum sculpturatum urgonense Razzauti, 1919	E	1	0	0	0	0	0	0	0
Opatrum sculpturatum caprariense Razzauti, 1919	E	0	1	0	0	0	0	0	0
Opatrum sculpturatum s.l. Fairmaire, 1860	W	0	0	0	1	0	0	0	0
Ammobius rufus (Lucas, 1846)	W	0	0	1	0	0	0	0	0
Trachyscelis aphodioides Latreille, 1809	W	0	0	1	1	1	0	0	0
Cossyphus tauricus Steven, 1832	W	0	0	0	0	0	0	1	0
Phaleria bimaculata bimaculata (Linné, 1767)	T	0	1	1	0	1	0	0	0
Phaleria revellierii Mulsant & Rey, 1858	W	0	0	1	0	1	0	0	0
Phaleria provincialis intermedia Schuster, 1930	T	0	0	1	0	0	0	0	0
Crypticus gibbulus (Quensel, 1806)	W	0	0	0	0	1	0	0	0
Gnatocerus cornutus (Fabricius, 1798)	W	0	0	0	0	1	0	0	0
Tribolium castaneum (Herbst, 1797)	W	0	0	1	0	1	0	0	0
Tribolium confusum (Jacquelin du Val, 1861)	W	0	0	0	0	1	0	0	0
Palorus subdepressus (Wollaston, 1864)	W	0	0	1	0	0	0	0	0
Alphitobius diaperinus (Panzer, 1796)	W	0	0	0	0	1	0	0	0
Iphtiminus italicus italicus (Truqui, 1857)	T	0	0	0	0	0	1	0	0
Tenebrio obscurus Fabricius, 1792	W	0	0	0	1	1	0	0	0
Tenebrio molitor Linné, 1758	W	0	0	0	1	1	0	0	0
Accanthopus velikensis (Piller & Mitterpacher, 1783)	W	0	0	1	0	0	0	0	0
Catomus rotundicollis (Guérin-Méneville, 1825)	W	0	1	1	1	1	0	1	0
Helops caeruleus caeruleus (Linné, 1758)	W	0	0	1	0	1	0	0	0
Probaticus ebeninus ebeninus (Villa & Villa, 1838)	C	0	0	0	0	1	0	0	0
Nalassus dryadophilus (Mulsant, 1854)	W	0	0	1	0	0	0	0	0
Nalassus planipennis (Küster, 1850)	T	0	0	1	0	0	0	0	1
Nalassus assimilis (Küster, 1850)	W	1	1	1	0	1	0	0	0
Xanthomus pallidus (Curtis, 1830)	W	0	0	0	1	0	0	0	0
Odocnemis ruffoi osellai (Gardini, 1979)	E	0	0	0	0	0	1	0	0

on the Tuscan Archipelago but not in Corsardinia), as suggested by Dapporto & Cini (2007), in order to highlight the source areas (Tuscany or Corsardinia, respectively). For this analysis, the two endemic subspecies of *Asida luigionii* (which is a T species) were combined in order to highlight their obvious origin from a Tuscan species.

Recent and paleogeographical data about island isolation and areas are the same as in Dapporto & Cini (2007), with slight changes to the values of the Pleistocene areas of Pianosa, Elba, Giannutri and Mt Argentario. For the peninsula present in the Pleistocene, which connected Elba and Pianosa to the mainland, Dapporto & Cini (2007) calculated a total area of 1700 km^2, and then used this value for all islands that were connected to the mainland. Since an identical value of 1700 km^2 for all these islands is not realistic, the Pleistocene peninsula was divided into two sectors using minimum linear widths as an indication of highest impediment to faunal interchange between different portions of the peninsula, which yielded a value of about 1250 km^2 for Pleistocene Elba and 450 km^2 for Pleistocene Pianosa. Using a similar procedure, an area of about 450 km^2 was calculated for Giannutri and Mt Argentario.

Role of Recent and Pleistocene factors in determining species richness

Species richness was correlated with Recent and Pleistocene factors using a Spearman rank correlation (Dapporto & Cini, 2007). If paleogeography determined species richness in the Tuscan Archipelago, then Pianosa (which in the Pleistocene was connected to Elba and Tuscany) should have more species than all the other islands (except Elba) (Dapporto et al., 2007). In fact, this hypothesis is not well formulated, because the Pleistocene richness of Pianosa should have decreased when it became an island and was reduced in size. Thus, if paleogeography favoured island colonization and species accumulation, and its influence is not erased by the effect of current factors, Pianosa should not have a larger number of species than the other islands, but a larger number of species than predicted by its current area. To obtain the expected number of species for Pianosa a species-area relationship (SAR) using a power function ($S = CA^z$, where S is the number of species, A is area, and C and z are fitting parameters) with a non-linear fitting procedure (quasi-Newton algorithm) was used (Fattorini, 2006c). If colonization occurred via a land-bridge, Pianosa, as well as the other islands connected to Tuscany, should have more species than predicted by this function (i.e., positive residuals; Fattorini, 2006b) as a consequence of their larger area and greater accessibility during the Pleistocene. Calculations were done using STATISTICA software (version 6) (Statsoft, 2001).

Biogeographical relationships among islands

The Jaccard coefficient and cluster analysis with UPGMA were used to obtain a representation of the biogeographical similarities of the islands (Fattorini, 2002a; Fattorini & Fowles, 2005; Dapporto et al., 2007). A common problem with cluster analysis is that it is not independent of how the data is grouped. The UPGMA amalgamation rule minimizes the distortion of the original data matrix and is therefore particularly favoured in biogeographical studies (cf. Fattorini, 2009a). In addition to UPGMA an alternative method of grouping, a single-linkage algorithm, was applied. This is a space-contracting strategy that reveals only the most discrete variation among entities (i.e., disjunct clusters). Thus, the results from UPGMA clustering can be compared with those obtained from single-linkage to explore whether the data exhibits a discrete or continuous structure (McGarigal et al., 2000).

If affected by Recent geography, Pianosa and Montecristo should have a transitional fauna and be less biogeographically similar to the other islands, and have a very isolated position in the cluster analysis, especially when a single-linkage fusion is used. In contrast, if affected more by Pleistocene geography, Pianosa and Montecristo should be biogeographically more similar to Tuscany and other islands connected to Tuscany in the past (Dapporto et al., 2007; Fattorini, 2009a). Cluster analyses were done using STATISTICA software (version 6) (Statsoft, 2001).

Role of Recent and Pleistocene factors in determining biogeographical patterns

To determine the effect of current and historical factors on biogeographical patterns Mantel tests were applied to matrices of biogeographical distances (i.e., Jaccard dissimilarities) between islands and the following island characteristics: (1) Recent inter-island isolation; (2) Pleistocene inter-island isolation; (3) Recent isolation from Corsica and Tuscany; (4) Pleistocene isolation from Corsica and Tuscany; (5) Recent ecological distances between islands; and (6) Pleistocene ecological distances between islands. Recent and Pleistocene inter-island isolations were measured as minimal sums of distances across the sea between islands, while Recent and Pleistocene isolations from Corsica and Tuscany were measured as Euclidean distances between islands based on the minimal sums of distances across the sea from Tuscany and Corsica-Sardinia; finally ecological distances were measured as Euclidean distances between islands based on measures of area and isolation standardized to Z-scores (see Dapporto & Cini, 2007, and Fattorini, 2009a for details). Matrices of explanatory variables that were significantly correlated to matrices of biogeographical distances by simple Mantel tests were used as third matrices in partial Mantel tests.

Although the use of Mantel tests has been questioned because it is difficult to express overall geographical and historical relationships among areas by simply using geographical distances or a dissimilarity coefficient (Fattorini, 2006a), more complex methods are not appropriate for the Tuscan Islands because of the small number of islands and variables involved.

Mantel and partial Mantel tests using Spearman rank correlation (r_s) were used in order to avoid problems associated with non-linear relationships. For each correlation, probability values were assessed using one-tailed tests with $P < 0.05$ from 1,000 randomizations. Calculations were done using XLSTAT software version 2008.3.02 (Addinsoft, 2008).

Although many tests were done, in accordance with the suggestions of Moran (2003), I did not apply the Bonferroni correction, but focused on P-values and consistence of results.

RESULTS

Faunal composition

For C and T species some characteristic patterns are apparent. *Stenosis angusticollis*, *Dichillus corsicus* complex and *Asida longicollis* are typically Corsardinian species (Fig. 1a–c), whereas *Asida luigionii*, *Colpotus strigosus* and *Nalassus planipennis* are typically Italian species (Fig. 2b–d). Finally, the peculiar distribution of *Opatrum sculpturatum* stretches from Mediterranean France to Tuscany and includes Northern Corsica (Fig. 2a). No T taxa are known among the tenebrionids of Montecristo. However, this island has two endemic subspecies (*Asida luigionii insularis*, which also occurs on other Tuscan Islands, and *Colpotus strigosus oglasensis*,

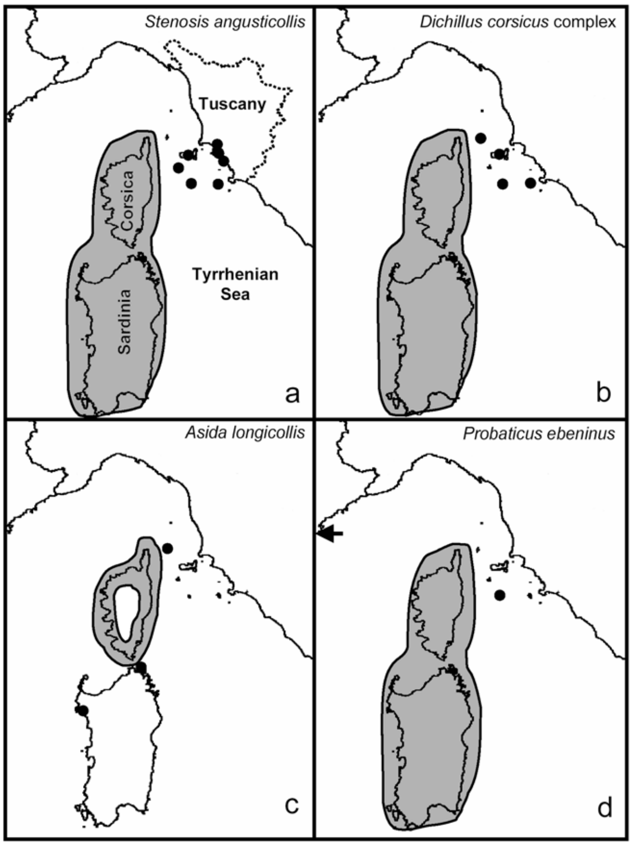

Fig. 1. Characteristic distributions of some species inhabiting the Tuscan Archipelago. The arrow in Fig. 1d indicates localities in South-Western France.

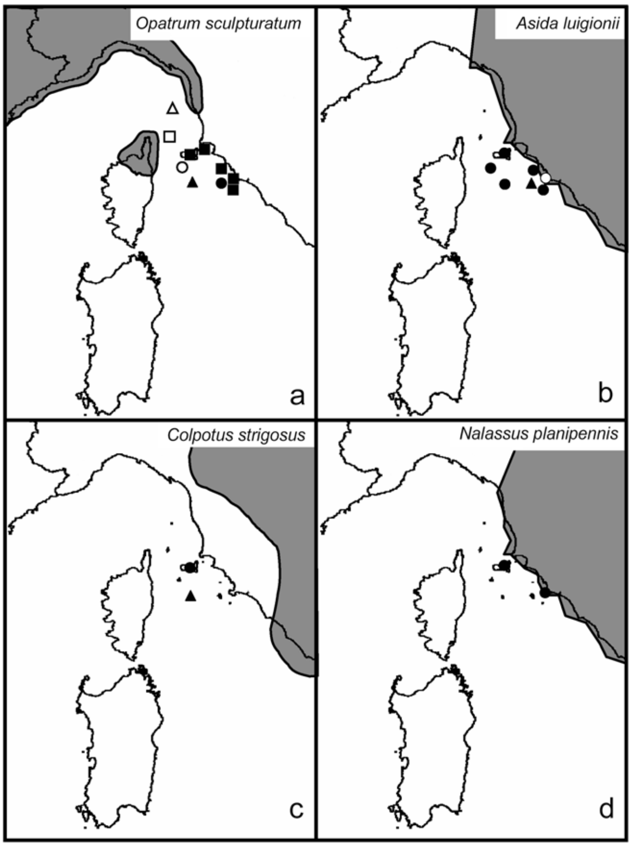

Fig. 2. Characteristic distributions of some species inhabiting the Tuscan Archipelago. Subspecies are indicated by different symbols. Fig. 2a: *Opatrum sculpturatum ilvense*: solid squares; *O. s. urgonense*: white triangle; *O. s. caprariense*: white square; *O. sculpturatum* ssp. from Montecristo: solid triangle; *O. s. igiliense*: solid circle; *O. s. sculpturatum sculpturatum*: white circle and grey areas. Fig. 2b: *Asida luigionii luigionii*: grey areas and white circle; *Asida l. insularis*: solid circles (taxon of disputed validity); *Asida l. doriae*: solid triangle. Fig. 2c: *Colpotus strigosus strigosus*: grey areas and solid circle; *C. s. oglasensis*: solid triangle.

which occurs only on this island, Fig. 1c) which are related to species occurring in Tuscany but not Sardinia or Corsica. If these subspecies are included among the T taxa, Montecristo has a markedly Tuscan fauna, as expected if the Pleistocene effect is dominant.

Some tenebrionid taxa are represented by populations endemic to individual islands or to groups of a few islands, such as *Asida luigionii* (with two subspecies, *doriae* and *insularis*) (Fig. 2b), the endemic *A. gestroi* (with the subspecies *gestroi*, *tyrrhena*, *caprariensis*, *lanzai* and *gardinii*), and *Opatrum sculpturatum* (with the endemic subspecies *ilvense*, *urgonense*, *caprariense* and *igiliense*) (Fig. 1a). However, out of the 13 tenebrionids endemic to the Tuscan Islands, only one (*Asida gestroi*) is a species and the others are subspecies, which suggests recent isolation.

Role of Recent and Pleistocene factors in determining species richness

Tenebrionid species richness is positively correlated with Recent island area ($r_s = 0.755$, $P = 0.03$ for all native species and even when anthropophilous species are excluded from the analysis; $r_s = 0.918$, $P = 0.001$ for CT species).

Using a power function to model SARs, Recent island area explained a high proportion of the variance ($S = 6.910A^{0.278}$, $R^2 = 0.673$ for all native species; $S = 6.177A^{0.282}$, $R^2 = 0.749$ for the data set with anthropophilous species excluded; and $S = 1.838A^{0.371}$, $R^2 = 0.928$ for CT species). Analysis of residuals showed that Pianosa and Giglio had the largest values in all SARs (about 6 species for Pianosa and 5 for Giglio for all native species; 4 and 3 species respectively for the reduced data set with anthropophilous species excluded; and 2 and 1 species respectively for CT species).

Using Pleistocene areas, SARs gave a poor fit to the data in all cases ($S = 5.932A^{0.194}$, $R^2 = 0.260$ for all native species; $S = 5.160A^{0.201}$, $R^2 = 0.308$ for the reduced data set with anthropophilous species excluded; and $S = 1.138A^{0.308}$, $R^2 = 0.400$ for CT species). In these cases, Pianosa showed small negative values.

Biogeographical relationships among islands

Cluster analyses of all native species after applying the UPGMA amalgamation rule produced a chained dendrogram (Fig. 3 a), where islands were placed according to their species richness, the more isolated islands have fewer species (Montecristo, Gorgona, Giannutri and Mt Argentario). The use of a single-linkage algorithm gave a

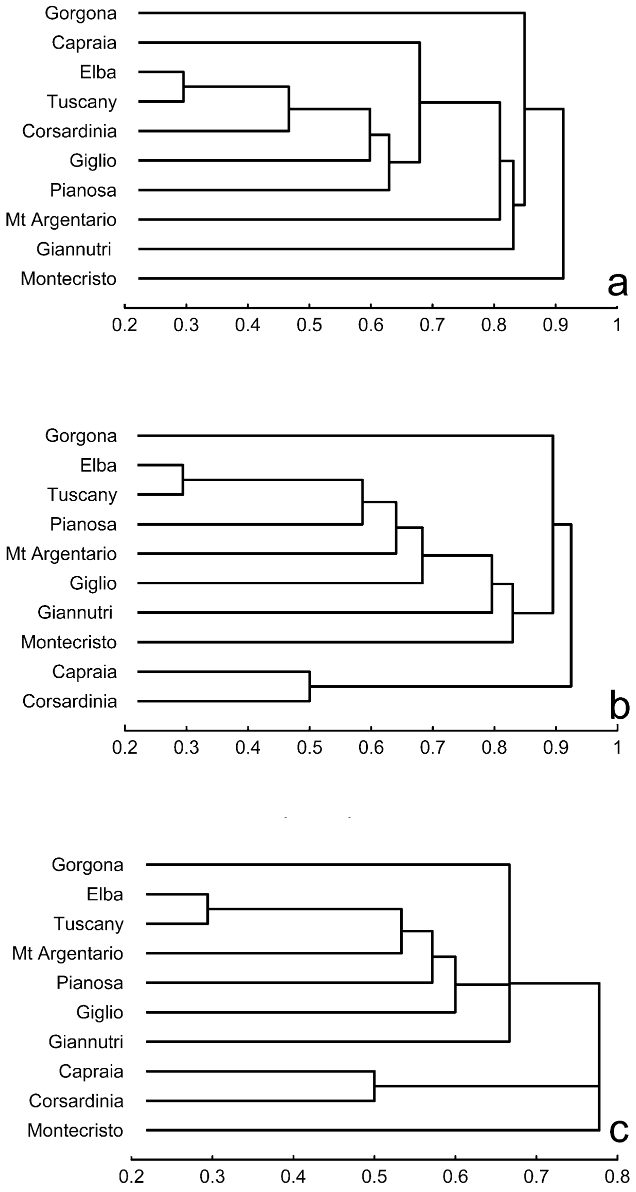

Fig. 3. Cluster analyses based on Jaccard dissimilarities showing patterns of tenebrionid biogeographical relationships among the Tuscan Islands. Fig. 3a was obtained assuming all populations are native and using the UPGMA amalgamation rule. The use of single-linkage or the exclusion of anthropophilous species, which are thought to be recent introductions, resulted in similar dendrograms. When widely distributed species were removed, cluster analyses using UPGMA (Fig. 3b) and single-linkage (Fig. 3c) gave very different results.

very similar result, with the remarkable difference that Pianosa is directly linked to the Elba-Tuscany-Corsardinia cluster. When anthropophilous species were excluded, both UPGMA and single-linkage cluster analyses produced results virtually identical to the dendrogram obtained using all native species and UPGMA grouping of data. Cluster analysis based on CT species and UPGMA grouping of data revealed a close relationship between Corsardinia and Capraia, and among Tuscany, Elba, Pianosa, Mt Argentario and Giglio (Fig. 3b). These two clusters were also recovered by the single-linkage clustering, which, however, indicated a more isolated position for Montecristo (Fig. 3c).

Role of Recent and Pleistocene factors in determining biogeographical patterns

Using Mantel tests, dissimilarities between islands in tenebrionids were significantly correlated with both Recent and Pleistocene geography (Recent geography: $r_s = 0.393$, $P = 0.021$ for all native species; $r_s = 0.415$, $P = 0.015$ excluding anthropophilous species; and $r_s = 0.464$, $P = 0.007$ for CT species; Pleistocene geography: $r_s = 0.413$, $P = 0.017$ for all native species; $r_s = 0.431$, $P = 0.012$ excluding anthropophilous species; and $r_s = 0.554$, $P = 0.002$ for CT species). Partial Mantel tests controlled for Pleistocene geography only revealed a weak correlation with Recent geography for CT species ($r_s = 0.235$, $P = 0.041$). However, partial Mantel tests controlled for Recent geography revealed a significant correlation between Jaccard dissimilarities and Pleistocene geography ($r_s = 0.285$, $P = 0.017$ for all native species; and $r_s = 0.262$, $P = 0.024$ excluding anthropophilous species). In addition, for CT species, there is a significant correlation with the Pleistocene distance to Corsardinia and Tuscany ($r_s = 0.543$, $P = 0.001$; $r_s = 0.254$, $P = 0.027$ when the effect of Recent geography was partialled out; $r_s = 0.269$, $P = 0.023$ when the effect of Pleistocene geography was partialled out). No influence of ecological distances was detected.

DISCUSSION

Recent papers on the Tuscan Archipelago (Dapporto et al., 2007; Dapporto & Cini, 2007; Dapporto & Strumia, 2008) conclude that the distribution of flying Hymenoptera and Lepidoptera, because of their high dispersal ability, is influenced mainly by present eco-geographical factors. This contrasts strongly with the general opinion that paleogeography (namely Pleistocene glacial maxima) is a key factor determining the distribution of plants and animals on these islands (see references in Mariotti, 1990 and in Dapporto & Cini, 2007).

In fact, current distributional patterns are the result of the interaction between historical (paleogeographical and paleoecological) and present (geographical and ecological) factors, and it is likely that their relative effect depends on the dispersal ability of the animal group considered. A recent comparative analysis of the biogeography of various animal groups on the Tuscan Islands revealed that highly mobile organisms (such as chrysidids and butterflies) were mostly influenced by current factors, while less mobile organisms (such as molluscs, reptiles and tenebrionids) were more influenced by historical factors (Fattorini, 2009a).

In the present paper, a study of the biogeography of tenebrionids identified Pleistocene geography (namely island characteristics and relationships during the glacial maxima) as an important determining factor of current distributional patterns.

The first piece of evidence comes from the SAR. As expected, tenebrionid species richness is positively correlated with current island area. This is expected because species richness tends to increase with area, possibly as a result of both current immigration/extinction processes and historical factors (Fattorini, 2007b). However, if current immigration is a key factor determining species richness on islands, a negative correlation with current isolation is expected (Fattorini, 2002b). Thus, lack of a correlation of tenebrionid richness with island isolation is evidence that tenebrionids are largely unable to cross even small stretches of water and that they colonized the islands probably via Pleistocene landbridges. Furthermore, Pianosa has more species than predicted by the SAR and when the origin of subspecies is included in the analysis the fauna of Montecristo has a high percentage of Tuscan species, which indicates these islands were mainly colonized in the Pleistocene. In particular, according to Dapporto et al. (2007), if paleogeography determined the species assemblages on the Tuscan Archipelago, then Pianosa and Montecristo should have a typical Tuscan fauna. In the cluster analyses Pianosa was consistently placed near Elba, while Montecristo was very isolated, as expected based on its current geography.

The general picture parallels the biogeographical patterns found in other groups, with Capraia mainly colonized from Corsica and Sardinia, and other islands from Tuscany, but this "biogeographical paradigm" is not evidence of a Pleistocene effect, because it is equally likely that it can be accounted for by both historical and current geographical factors (Dapporto & Strumia, 2008). As a matter of fact, Mantel tests indicate significant correlations of biogeographical distances with both Recent and Pleistocene geography. However, when the influence of Recent geography was partialled out, Pleistocene geography was still correlated with biogeographical distances, while the influence of Recent geography disappeared when Pleistocene geography was partialled out. This suggests that the influence of Pleistocene geography is stronger than that of Recent geography.

The incidence of endemic taxa also indicates that Pleistocene geography is important. During the Würm Pleistocene sea regression, Elba (31 taxa, 2 endemics, 6.5%) and Pianosa (16 taxa, 1 endemic, 6.3%) formed a single landmass connected to the Italian mainland. Note that the taxon on Pianosa which is endemic to Tuscan Islands is unique to this island, while the two endemic taxa of Elba are also found on other Tuscan Islands. Giannutri (8 taxa, 1 endemic, 13%) and possibly Giglio (18 taxa, 2 endemics, 11%) were also connected to the mainland. However, while the endemic taxon on Giannutri is not unique to that island, the two endemic taxa on Giglio are unique to that island, which suggests that these islands were isolated from the mainland prior to the Pleistocene. Mt Argentario, which is part of the Tuscan mainland, has a low level of endemicity (12 taxa, 1 endemic, 8%), with no unique endemic taxon. Capraia (15 taxa, 2 endemics, 13%), Gorgona (8 taxa, 2 endemics, 25%) and Montecristo (9 taxa, 4 endemic taxa, 44%) were isolated from one another during the Pleistocene and share the highest levels of endemism, with unique endemics (2 on Capraia, 1 on Gorgona and 3 on Montecristo). As a whole, the islands that have been isolated for a long time show high levels of endemism. For these islands, the shared endemics could have resulted from pre-Pleistocene land connections. In particular, *Opatrum sculpturatum* shows a high evolutionary plasticity on the Tuscan Islands and its distribution indicates a relict origin, possibly dating to before the disjunction of the Corsardinian microplate (cf. Fattorini, 2008d), followed by dispersal to the Tuscan Islands. The distribution of *Probaticus ebeninus* (Fig. 1d) also fits this pattern.

The relict distribution of relatively sedentary organisms should be matter of concern for conservation biogeographers, because local species extinction is not easily compensated by immigration (cf. Fattorini, 2008b). Thus, although island populations of species with high dispersal power can be at least partially reconstituted by new immigrants from adjacent source areas, tenebrionids may be more vulnerable to extinction as they mostly originated via land connections with the mainland and cannot now be balanced by new immigrations from mainland populations.

According to Dapporto and coworkers (Dapporto et al., 2007; Dapporto & Cini, 2007) human activity probably affects the natural turnover of species assemblages by increasing extinction rates and favouring colonization by widespread species, and conceals the role of historical factors in the current composition of chrysidid and butterfly species. This is even more true for tenebrionids as it cannot be excluded that endemic taxa associated with wooded areas were lost when the oak forests were destroyed (Fattorini, 2008c).

At present, the human population on the Tuscan Islands is relatively small and declining (e.g., de Fabrizio, 2005), thus the most important threat is from the effects of tourism. All the islands studied are in the Tuscan Archipelago National Park. Access to Montecristo, Gorgona and Pianosa is strictly regulated and therefore these islands are less threatened. However, other islands are subject to high pressure from tourists, notably Elba and Giglio, which are important tourist destinations. A serious consequence of mass tourism and even so-called ecotourism is the rapid degradation of fragile natural habitats, which are becoming more and more attractive to tourists just because of their increasing rarity. This is the case of the few and scattered sandy shores on Giglio, now completely obliterated by bathing establishments, or, in the case of the small and very isolated beaches, constantly visited by single tourists. The psammophilous species *Phaleria* spp. and *Trachyscelis aphodioides* are now considered to be extinct on this island. Increasing rarity of well-preserved places led to high pressure from tourists also on the Island of Giannutri. Although tourists are forbidden to use most of the footways on this island, most tourists are unaware of this and those that reach the island by ferry-boats concentrate in the few accessible places.

The high incidence of anthropophilous and cosmopolitan species on Giglio is evidence of the influence of man on the tenebrionid communities. Although recent field studies on Giglio (from 1998 to 2008) indicate that endemic or localized taxa, such as *Dichillus corsicus*, *Dendarus coarcticollis*, *Helops caeruleus*, *Asida luigionii doriae* and *Opatrum sculpturatum igiliense*, can still easily be found, the most frequently encountered species are those of the genus *Blaps* and the highly eurytopic *Pedinus meridianus* and *Scaurus striatus* (S. Fattorini, pers. observ.).

The continued effect of man on the Tuscan Islands has resulted in new habitats, which may also be of conservation value for tenebrionids. For example, old buildings offer shelter for various species, such as *Stenosis sardoa* and *Asida luigionii luigionii*, and the endemic *Asida luigionii doriae*, *Asida gestroi* and subspecies of *Opatrum sculpturatum*, as well as anthropophilous species, such as *Akis bacarozzo*, *Scaurus striatus* and *Blaps* spp. (Gardini, 1976; S. Fattorini, pers. observ. on Giglio). This is also the case of plane trees (*Platanus* sp.), which were frequently planted as ornamental plants. Plane trees shed their bark regularly. If the outer part of the bark is shed but not detached from the trunk, it provides suitable resting places for a number of insects, as is commonly recorded for *Eucalyptus* trees (cf. Fattorini, 2008c). For example, *Stenosis brenthoides*, *Dendarus coarcticollis*, *Colpotus strigosus* and *Accanthopus velikensis* were found under loose bark of plane trees on Elba (Gardini, 1976).

Thus, although conservation and restoration usually involves the destruction of introduced plants and man-made habitats, their potential as habitats for endemic and anthropophilous species needs to be evaluated.

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REFERENCES

Addinsoft 2008: *XLSTAT Version 2008.3.02* [www.xlstat.com].

Baroni Urbani C. 1971: Studien zur Ameisenfauna Italiens XI. Die Ameisen des Toskanischen Archipels. Betrachtungen zur Herkunft der Inselfaunen. *Rev. Suisse Zool.* **78**: 1037–1067.

Chatzimanolis S., Trichas A., Gioaks S. & Mylonas M. 2003: Phylogenetic analysis and biogeography of Aegean taxa of the genus Dendarus (Coleoptera: Tenebrionidae). *Insect Syst. Evol.* **34**: 295–312.

Dapporto L. & Cini A. 2007: Faunal patterns in the Tuscan archipelago butterflies: The dominant influence is recent geography not paleogeography. *Eur. J. Entomol.* **104**: 497–503.

Dapporto L. & Strumia F. 2008: A rapid assessment of Lepidoptera biogeography in the Tuscan Archipelago using economical Malaise traps. *Ital. J. Zool.* **75**: 219–224.

Dapporto L., Wolf H. & Strumia F. 2007: Recent geography determines the distribution of some flying Hymenoptera in the Tuscan Archipelago. *J. Zool.* **272**: 37–44.

De Fabrizio E. 2005: *Isola del Giglio. Il territorio, gli abitanti e la storia*. Proloco dell'Isola del Giglio, Grosseto, Italy, 272 pp.

Fattorini S. 2002a: Biogeography of the tenebrionid beetles (Coleoptera, Tenebrionidae) on the Aegean Islands (Greece). *J. Biogeogr*. **29**: 49–67.

Fattorini S. 2002b: Relict versus dynamic models for tenebrionid beetles of Aegean Islands (Greece) (Coleoptera: Tenebrionidae). *Belgian J. Zool.* **132**: 55–64.

Fattorini S. 2006a: Spatial patterns of diversity in the tenebrionid beetles (Coleoptera, Tenebrionidae) of the Aegean Islands (Greece). *Evol. Ecol. Res.* **8**: 237–263.

Fattorini S. 2006b: Detecting biodiversity hotspots by species-area relationships: a case study of Mediterranean beetles. *Conserv. Biol.* **20**: 1169–1180.

Fattorini S. 2006c: To fit or not to fit? A poorly fitting procedure produces inconsistent results when the species-area relationship is used to locate hotspots. *Biodiv. Conserv.* **16**: 2531–2538.

Fattorini S. 2006d: Biogeography and conservation of endemic tenebrionid beetles (Coleoptera: Tenebrionidae) on East Mediterranean islands. *Vie Milieu* **56**: 231–241.

Fattorini S. 2007a: Levels of endemism are not necessarily biased by the co-presence of species with different range sizes: a case study of Vilenkin & Chikatunov's models. *J. Biogeogr.* **34**: 994–1007.

Fattorini S. 2007b: Non-randomness in the species-area relationship: testing the underlying mechanisms. *Oikos* **116**: 678–689.

Fattorini S. 2008a: A multidimensional characterization of rarity applied to the Aegean tenebrionid beetles (Coleoptera: Tenebrionidae). *J. Insect Conserv*. **12**: 251–263.

Fattorini S. 2008b: How island geography and shape may influence species rarity and biodiversity loss in a relict fauna: a case study of Mediterranean beetles. *Open Conserv. Biol. J.* **2**: 11–20.

Fattorini S. 2008c: Ecology and conservation of tenebrionid beetles in Mediterranean coastal areas. In Fattorini S. (ed.): *Insect Ecology and Conservation*. Research Signpost, Trivandrum, pp. 165–297.

Fattorini S. 2008d: Hovenkamp's ostracized vicariance analysis: testing new methods of historical biogeography. *Cladistics* **24**: 611–622.

Fattorini S. 2009a: Both recent and Pleistocene geography determines animal distributional patterns in the Tuscan Archipelago. *J. Zool.* **277**: 291–301.

Fattorini S. 2009b: On the General Dynamic Model of oceanic island biogeography. *J. Biogeogr.* (in press).

Fattorini S. & Fowles A. 2005: A biogeographical analysis of the tenebrionid beetles (Coleoptera, Tenebrionidae) of the island of Thasos in the context of the Aegean Islands (Greece). *J. Nat. Hist.* **39**: 3919–3949.

Fattorini S. & Leo P. 2000: Darkling beetles from Mediterranean minor islands: new records and biogeographical notes (Coleoptera Tenebrionidae). *Boll. Soc. Entomol. Ital.* **132**: 205–217.

Ferrer J. 2008: Contribución al conocimiento de los Asidini iberobaleares. Segunda nota. Las Alphasida (Glabrasida) del grupo Tricostatae Escalera 1922 (Coleoptera, Tenebrionidae, Pimeliinae). *Boln. S.E.A.* **43**: 61–73.

Gardini G. 1976: Materiali per lo studio dei Tenebrionidi dell'Arcipelago Toscano (Col. Heteromera). *Lav. Soc. Ital. Biogeogr*. **5**: 637–723.

Gardini G. 1979: Nuovi dati sui Tenebrionidi (Col.) dell'Arcipelago Toscano. *Boll. Mus. Civ. St. Nat. Verona* **6**: 73–77.

Isaac N.J.B. & Purvis A. 2004: The species problem and testing macroevolutionary hypotheses. *Divers. Distrib.* **10**: 275–281.

Leo P. 1998: Nuovi dati sui tenebrionidi delle isole toscane e descrizione di Asida (s. str.) gestori Leoni lanzai n. sp. (Coleoptera, Heteromera). *Atti Mus. Stor. Nat. Maremma* **17**: 73–77.

Löbl I. & Smetana A. (eds) 2008: *Catalogue of Palaearctic Coleoptera. Vol. 5. Tenebrionoidea*. Apollo Books, Stenstrup, 670 pp.

Lo Cascio P., Bartolozzi L., Cecchi L., Dapporto L. & Sforzi A. 2000: Contributi alla conoscenza dell'artropodofauna dell'Isola di Pianosa (Arcipelago Toscano). 3. Coleoptera Tenebrionidae. *Boll. Soc. Entomol. Ital.* **132**: 157–174.

MacArthur R.H. 1972: *Geographical Ecology. Patterns in the Distribution of Species.* Princeton University Press, Princeton, 269 pp.

MacArthur R.H. & Wilson E.O. 1967: *The Theory of Island Biogeography*. Princeton University Press, Princeton, 203 pp.

McGarigal K., Cushman S. & Stafford S. 2000: *Multivariate Statistics for Wildlife and Ecology Research*. Springer, New York, 283 pp.

Mariotti M. 1990: Floristic connections between the Sardo-Corsican Dominion and the Ligurian area. *Atti Conveg. Accad. Naz. Lincei* **85**: 429–448.

Moran M.D. 2003: Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **100**: 403–405.

Morey M. & Martínez-Taberner A. 2000: Environmental conservancy strategies in the Mediterranean islands. In Trabaud L. (ed.): *Life and Environment in the Mediterranean*. Wit-Press, Southampton, pp. 345–386.

Piantelli F., Giusti F., Bernini F. & Manganelli G. 1990: The mollusc and oribatid fauna on the Aeolian and Tuscan archipelagos and the island equilibrium theory. *Atti Conveg. Accad. Naz. Lincei* **85**: 117–154.

Ryder O.A. 1986: Species conservation and systematics: the dilemma of subspecies. *Trends Ecol. Evol.* **1**: 9–10.

Samways M.J. 1998: Insect population changes and conservation in the disturbed landscapes of Mediterranean-type ecosystems. In Rundel P.W., Montenegro G. & Jaksic F.M. (eds): *Landscape Disturbance and Biodiversity in Mediterranean-type Ecosystems*. Springer, Berlin, pp. 313–331.

Società Italiana di Biogeografia (ed.) 1974: Il popolamento animale e vegetale dell'Arcipealgo toscano. Atti del XX Congresso della Società Italiana di Biogeografia. Vol. 5. *Lav. Soc. Ital. Biogeogr*. **5**.

StatSoft Inc. 2001: *STATISTICA (Data Analysis Software System). Version 6.* Computer program manuals. Tulsa, OK [www.statsoft.com].

Whittaker R.J. 1998: *Island Biogeography: Ecology, Evolution, and Conservation.* Oxford University Press, Oxford, 285 pp.

Whittaker R.J., Araújo M.B., Jepson P., Ladle R.J., Watson J.E.M. & Willis K.J. 2005: Conservation Biogeogarphy: assessment and prospect. *Divers. Distrib.* **11**: 3–23.

Whittaker R.J., Triantis K.A. & Ladle R.J. 2008: A general dynamic theory of oceanic island biogeography. *J. Biogeogr.* **35**: 977–994.

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