

Ecological and historical factors affecting carabid and tenebrionid communities (Coleoptera Carabidae and Tenebrionidae) in a Mediterranean coastal area

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SUMMARY

This research aimed to compare the diversity of carabid and tenebrionid communities in a Mediterranean area (Castelporziano, Central Italy), searching for the historical and ecological factors responsible for the observed patterns. In the study area, carabids showed the highest richness values in wetlands and in open areas, while tenebrionids were more speciose on the dune and in the natural forest. As to the carabids, stenotopic species occurred in the beach-dune system, in the mesophilous forest, and, with very high proportions, in wetlands and in open areas. By contrast, in the tenebrionids, the stenotopic species were strongly represented on the dune, in wetlands, in the oak forest, and poorly in open areas. As a whole, most of the carabid species are distributed in the Palearctic region, while most of the tenebrionids are distributed in the Mediterranean area. For the carabids, the stenotopic species were mostly represented by species widely distributed in the Palearctic area, while for the tenebrionids the stenotopic species were mostly represented by species distributed in the Mediterranean region. This can be explained by the fact that, in contrast with carabids (where stenotopic species are nearly all hygrophilous), stenotopic tenebrionids include at least two categories: stenotopic species associated with sandy soils, and stenotopic species associated with trees. From an ecological point of view, the occurrence of many carabid species with Palearctic chorotypes (which are also typically stenotopic hygrophilous species) can be related to the presence of wetlands and ponds. Most probably, such species largely colonised Italian coastal areas during Pleistocene glaciations, as a consequence of a colder climate that favoured dispersal processes from northern and inland regions. The occurrence of many thermophilous species with Mediterranean chorotypes among the tenebrionids can be related to the Mediterranean feature of the area and to the refugial role of the Tyrrhenian coasts during Pleistocene glaciations. The present occurrence of some tenebrionid species with 'northern' chorotypes can be related to the presence, in the study area, of hygrophilous/mesophilous phytoceenoses.

INTRODUCTION

Carabidae and Tenebrionidae are very speciose in Italy. Carabidae include approximately 1300 species (Vigna Taglianti, 1993), Tenebrionidae 255 species (Fattorini and Maltzeff, 2001). Both Carabidae and Tenebrionidae are excellent models for biogeographical purposes (Fattorini, 2000, 2002a, 2002b; Vigna

Taglianti, 1998; Casale and Vigna Taglianti, 1999). However, they are very different in their general ecology. Carabidae are typically predaceous insects, especially linked to wetlands (e.g., Thiele, 1977), while Tenebrionidae are typically detritivores, sometimes highly specialised to life in arid environments, where they may represent a prominent part of the fauna (Fattorini, 2000).

Carabidae and Tenebrionidae represent a conspicuous faunal component of coastal areas in the Mediterranean (e.g., Vigna Taglianti and Fattorini, 2002; Carpaneto and Fattorini, 2001). Both the families include some species linked to the beach-dune ecosystem, as well as a number of species inhabiting maquis, prairies and woodlands. These ecological characteristics make Carabidae and Tenebrionidae very useful taxa for ecological and biogeographical researches in Mediterranean coastal areas, where a mosaic of vegetation types generally occurs.

The protected area of Castelporziano is a well preserved Tyrrhenian coastal area with a high diversified vegetation, including psammophilous plant associations, maquis, oak forests, hygrophilous forests and steppe areas. This complex vegetation obviously offers a number of habitats for insects with different ecological preferences, such as those belonging to the families Carabidae and Tenebrionidae.

We have recently published two papers on these two families at Castelporziano (Vigna Taglianti et al., 2001; Fattorini and Maltzeff, 2001). Using data presented in these two papers, we attempted here to compare the diversity of carabid and tenebrionid communities from different points of view, searching for the historical and ecological factors responsible for the observed patterns. In particular, we compared: (1) the species richness of the two families in different habitats; (2) their beta-diversity; (3) their ecological composition; and (4) their zoogeographic characterisation.

MATERIALS AND METHODS

The study area (Castelporziano Presidential Estate) is a natural reserve located about 20 km South of Rome (Central Italy). It covers an area of *ca* 6086 hectares.

The area lies on the sandy soils of the mouths of the Tevere River. Beside a pine (*Pinus pinea*) forest, and a man-made mesophilous forest, the forest vegetation of this area is prevalently represented by fragments of oak (*Quercus ilex*) woods, with some patches occupied by *Q. suber* and *Q. robur* woods. Temporary and permanent ponds, with associated vegetation types, are widely scattered through the entire area. Along the coast, shrubby sclerophyllous associations and dune vegetation occur.

As a whole, the following main habitat types can be recognised: (1) beach, (2) dunes, (3) low maquis, (4) high maquis, (5) wetlands, (6) natural (oak) forests, (7) man-made (mesophilous) forests, (8) steppes and cultivated plots (open areas).

To compare the carabid and tenebrionid species richness of the main habitats of Castelporziano, a matrix of presence/absence of each species in each habitat

was compiled (Tables I and II). According to their occurrence in the different habitats at Castelporziano, the species were grouped into the following three ecological categories: (1) stenotopic (species strictly associated with one habitat); (2) oligotopic (species associated with two habitats); (3) eurytopic (species occurring in more than two habitats). Note that Fattorini and Maltzeff (2001) and Fattorini (2002c) used the same terms: steno-, oligo- and eurytopic in a different way. These authors used such terms in reference to the habitat breadth of the species in Central Italy. We used here the same terms only in reference to their habitat breadth in the study area.

As a measure of beta-diversity (i.e., the extent of species replacement among habitats) we used the index proposed by Wittaker: $\beta = s/\alpha' - 1$, where s is the total number of species recorded in the study system, and α' is the average number of species found within the community samples (for the purposes of this paper, α' is the average number of species found in each of the eight habitats cited above). According to Wilson and Shmida (1984), this index is one of the most suitable measures of beta-diversity and it is the measure of choice when samples cannot be arranged along a single gradient. This is the case of Castelporziano, where the habitats (samples) have a mosaic distribution.

To study if the distribution of the carabid species richness among habitats was significantly different from that of tenebrionids, we arranged a 8×2 contingency table (rows: habitats; columns: carabids and tenebrionids) resulting in the following χ^2 test:

$$\chi^2 = \sum_{i=1}^s \sum_{b=1}^t \frac{(n_{1b} - n_{1b}^*)^2}{n_{ib}^*} = n_{01} n_{02} \sum_{i=1}^s \frac{\left(\frac{n_{i1}}{n_{01}} - \frac{n_{i2}}{n_{02}} \right)^2}{n_{i0}}$$

where:

n = observed frequencies, n^* = expected frequencies, n_{01} = total number of carabid records, n_{02} = total number of tenebrionid records, n_{i1} = number of carabid species recorded in a given habitat, n_{i2} = number of tenebrionid species recorded in a given habitat, $n_{i0} = n_{01} + n_{02}$ for a given habitat.

Note that n_{01} and n_{02} are not the total number of carabid and tenebrionid species respectively, but the sum of the numbers of carabid and tenebrionid species observed in each habitat.

This test follows a χ^2 distribution, with $s-1$ degrees of freedom. As $s = 8$, for $\alpha = 0.05$, the threshold values is $\chi^2_{7, 0.05} = 14.067$.

Chorotypes follow Vigna Taglianti et al. (1999). Chorotypes were grouped into the following distribution types of greater extent: 'Palearctic' = OLA, PAL, WPA, ASE, SIE, CEM, CAE, TEM, TUE, TUM; 'European' = EUR, SEU, EUM; 'Mediterranean' = MED, WME, EME; 'Afrotropical' = AIM, AFM, AFP (for acronyms see Table I).

For both carabids and tenebrionids we calculated the proportion of both different chorotypes and ecological categories (i.e., proportion of steno-, oligo- and eurytopic species). To study the possible relationships between geographical distribution types and ecological categories, we also calculated for each family: (1) the proportion of each ecological category in each distribution type; and (2) the proportion of each distribution type in each ecological category. The first analysis shows the ecological composition of the geographical patterns, while the second the geographical composition of the different ecological categories.

In all of these analyses, a χ^2 test was used to verify if the differences in species number among the chorological and ecological categories were significant, the null hypothesis being a uniform distribution. Thus, the expected values were calculated dividing the total number of carabid or tenebrionid species by the number of involved categories, while the observed values were the number of species belonging to each category. In certain cases, very small values of expected frequencies (< 5) prevented the use of the test. A sequential Bonferroni test was used to adjust the significance level to the number of comparisons using the same data set.

In order to study the contribution of different ecological categories to the community of each habitat, we calculated the proportion of steno-, oligo- and eurytopic species in each habitat for both carabids and tenebrionids. For both families, we arranged a 8×3 contingency table (rows: habitats; columns: ecological categories) which was subject to a χ^2 test similar to that used for testing differences in carabid and tenebrionid richness. In this case, we had $(s-1)(t-1)$ degrees of freedom (i.e., 14 df) and for $\alpha = 0.05$ a threshold value $\chi^2 = 14,0,005 = 23.685$.

To test if the contribution of 'northern' chorotypes (i.e., Palearctic + European distribution types) was statistically different between carabids and tenebrionids, we used the formula:

where: P_1 = proportion of 'northern' carabids, P_2 = proportion of 'northern' tenebrionids, n_1 = total number of carabid species, n_2 = total number of tenebrionid species, and

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

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

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

The same procedure was also used to test if the proportion of the carabid species richness in the study area on the entire Italian fauna was significantly different from that of tenebrionids.

The myrmecophilous tenebrionid *Oochrotus unicolor ardoini* Canzoneri, 1961, a W-Mediterranean species for which the habitat distribution in the study area is unclear, was excluded in all analyses, with the exception of those dealing with the zoogeographic whole spectrum.

RESULTS

The carabid beetle fauna of Castelporziano includes 175 species, i.e., ca 13% of the Italian fauna. The tenebrionid beetles collected in the same area include 38 species, i.e., ca 15% of the tenebrionid fauna in Italy. Thus, the proportion: number of collected species/number of species occurring in Italy is similar in the two families ($Z = -0.742$).

Looking at the species richness in the different habitats, carabids showed the highest richness values in wetlands and in open areas, while tenebrionids were more speciose on the dune and in the natural forest (Figs. 1, 2). The two patterns were significantly different ($\chi^2 = 79.164$, $df = 7$, $p < 0.001$).

The beta-diversity was greater in carabids ($\beta = 4.83$) than in tenebrionids ($\beta = 3.06$).

Carabid beetles showed a very high proportion of stenotopic species, followed by the oligotopic and eurytopic ones (Fig. 3) ($\chi^2 = 119.669$, $df = 2$, $p < 0.001$). Stenotopic species were the most represented category also in tenebrionids, but the eurytopic species were also strongly represented (Fig. 4) ($\chi^2 = 13.351$, $df = 2$, $p = 0.001$).

The proportion of the three categories in each habitat for the two families is shown in Figs. 5 and 6. For both families, the three ecological categories showed significant differences among habitats ($\chi^2 = 66.065$, $df = 14$, $p < 0.001$ for the carabids; $\chi^2 = 36.908$, $df = 14$, $p < 0.001$ for the tenebrionids). As to the carabids, the stenotopic species occurred in the beach-dune system, in the mesophilous forest, in wetlands, and, with very high proportions, in open areas. Oligotopic species roughly followed a similar pattern, while the eurytopic ones obviously followed an opposite pattern. By contrast, in the tenebrionids, the stenotopic

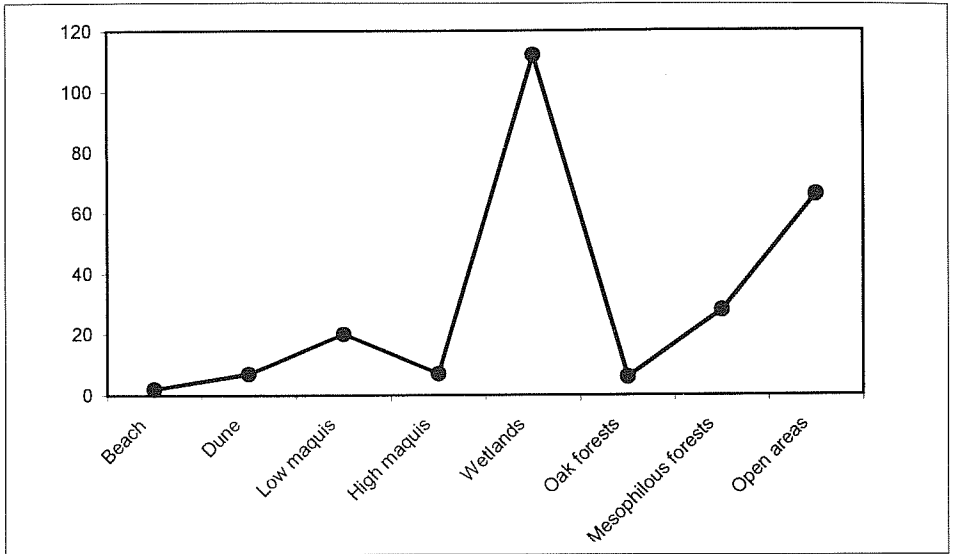


Fig. 1 - Carabid species richness in each habitat

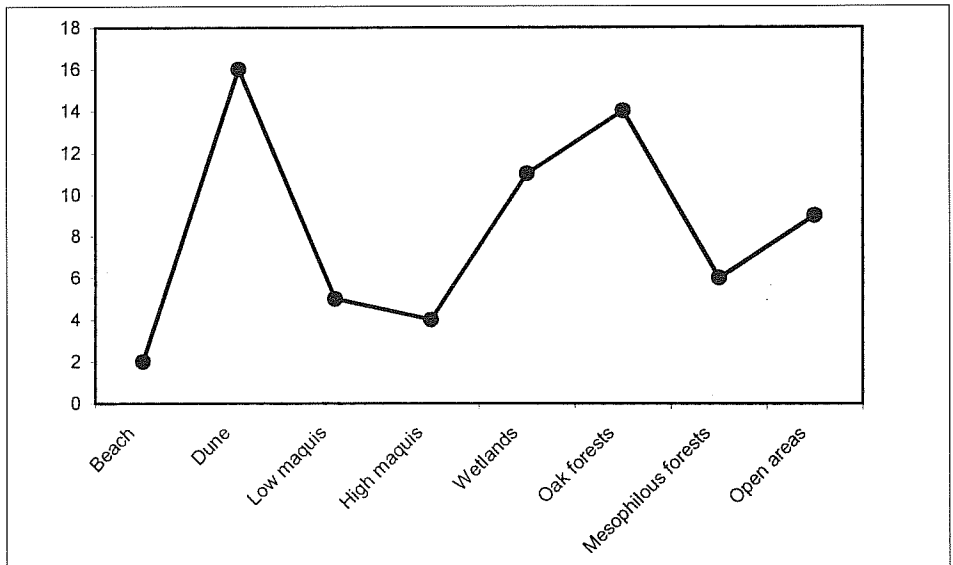


Fig. 2 - Tenebrionid species richness in each habitat

species were strongly represented on the dune, in wetlands, in the oak forest, and poorly in open areas (only one species).

The zoogeographic spectrum of the carabids occurring in the study area includes 19 chorotypes (Table I). These chorotypes were grouped into classes of

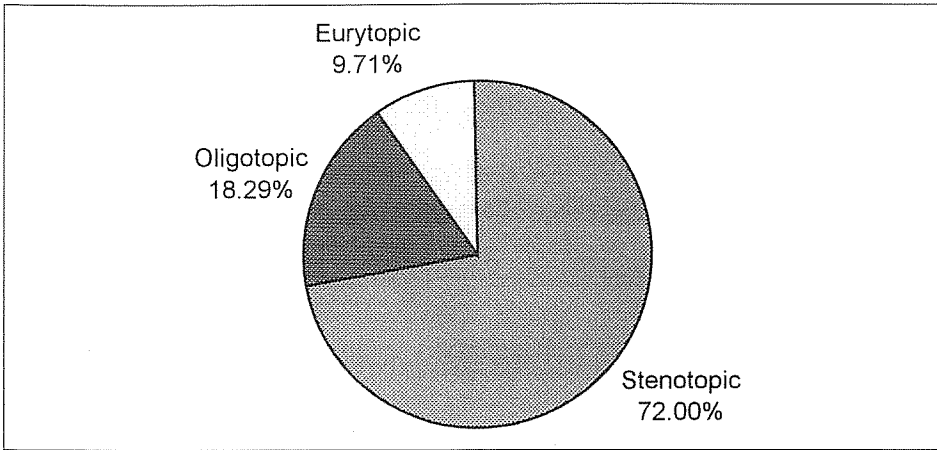


Fig. 3 - Proportion of steno-, oligo- and eurytopic carabid species

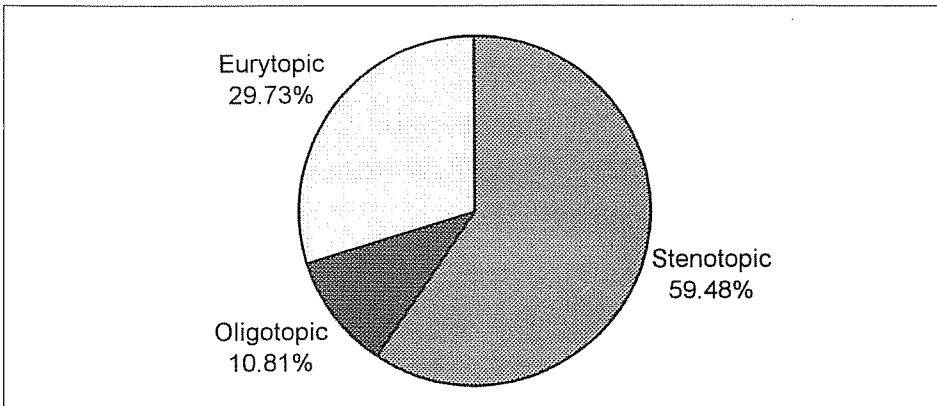
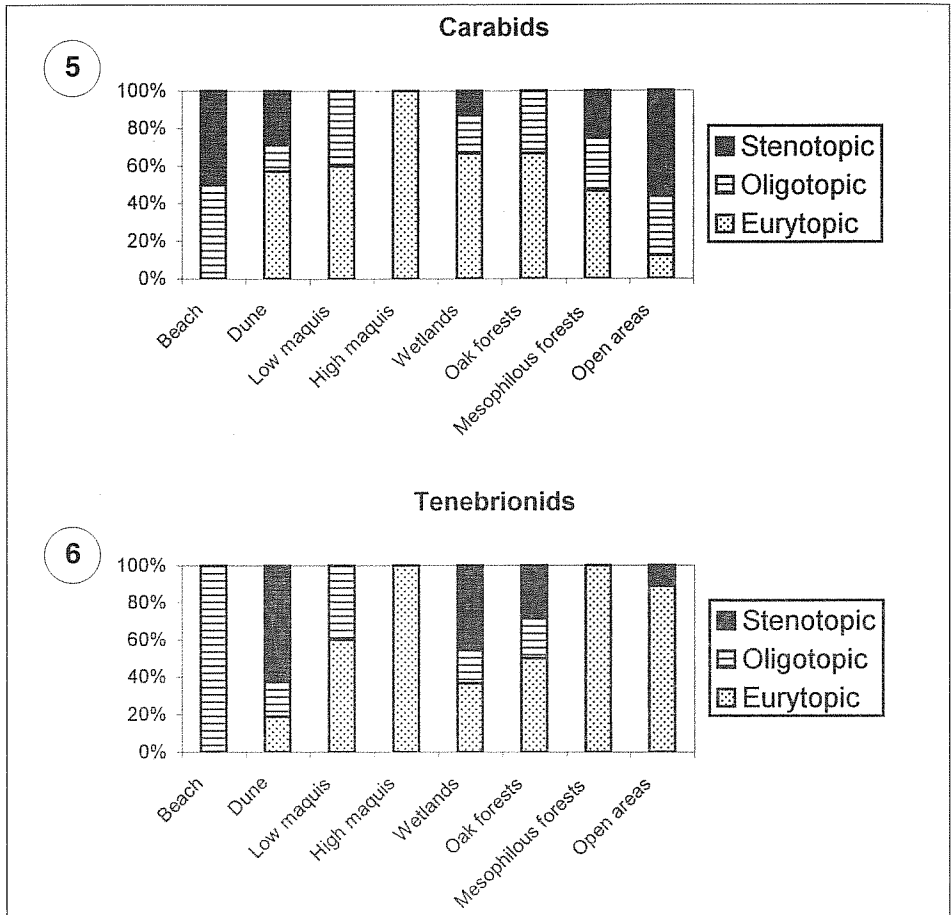


Fig. 4 - Proportion of steno-, oligo- and eurytopic tenebrionid species

wider meaning (Fig. 7): (1) species widely distributed in the Palearctic region ('Palearctic species'); (2) species distributed in Europe ('European species'); (3) species distributed in the Mediterranean ('Mediterranean species'); (4) species distributed in the Mediterranean and in the Afrotropical region ('Afromediterranean species'). As a whole, the frequencies of the different categories were significantly different ($\chi^2 = 10.366$, $df = 2$, $p = 0.006$). Most of the carabid species are widely distributed in the Palearctic region. The European component is also strongly represented, while the Mediterranean elements occur with a lower percentage.

The zoogeographic spectrum of the tenebrionids includes eight chorotypes (Table II). If the chorotypes are grouped into the same more general distribution types used for carabids, we can see that most of the species are distributed in



Figs. 5-6 - Proportion of steno-, oligo- and eurytopic species in each habitat

the Mediterranean. The species distributed in Europe are less represented, and those widely distributed in the Palearctic region are poorly represented (Fig. 8). Also for the tenebrionids, the frequencies of the different categories were significantly different ($\chi^2 = 10.158$, $df = 2$, $p = 0.006$).

The percentage of 'northern' chorotypes (i.e., Palearctic species + European species) in carabids (74.28%) greatly exceeds that of tenebrionids (44.73%) ($Z = 3.97$).

Figs 9-14 show the proportion of stenotopic, oligotopic and eurytopic species in each of the general distribution types for both families.

For the carabids, the distribution of steno-, oligo- and eurytopic species was significantly different from a uniform (1:1:1) distribution in all distribution types, the χ^2 values being $\chi^2 = 59.769$ ($df = 2$, $p < 0.001$) for the Palearctic species,

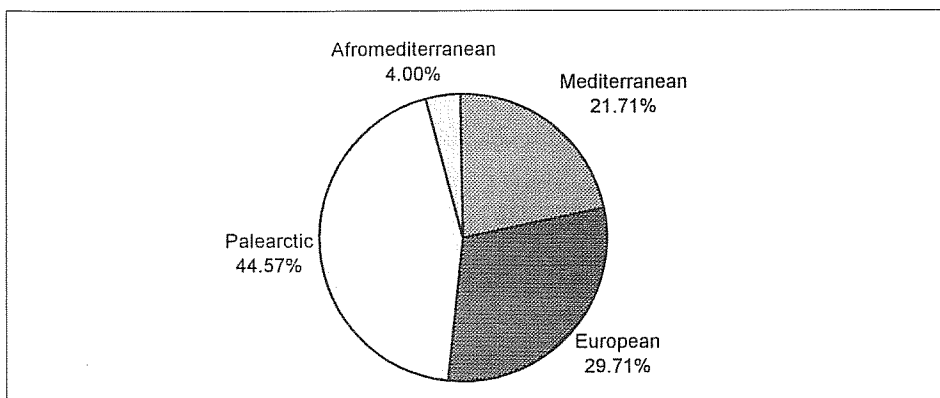


Fig. 7 - Zoogeographic spectrum of carabid beetles

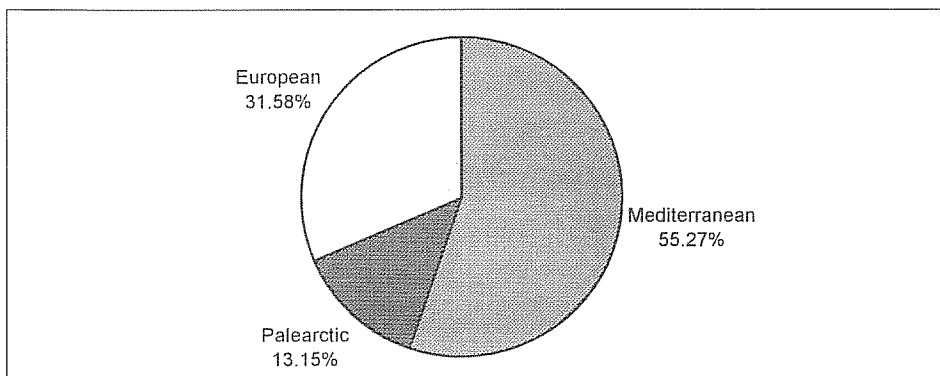
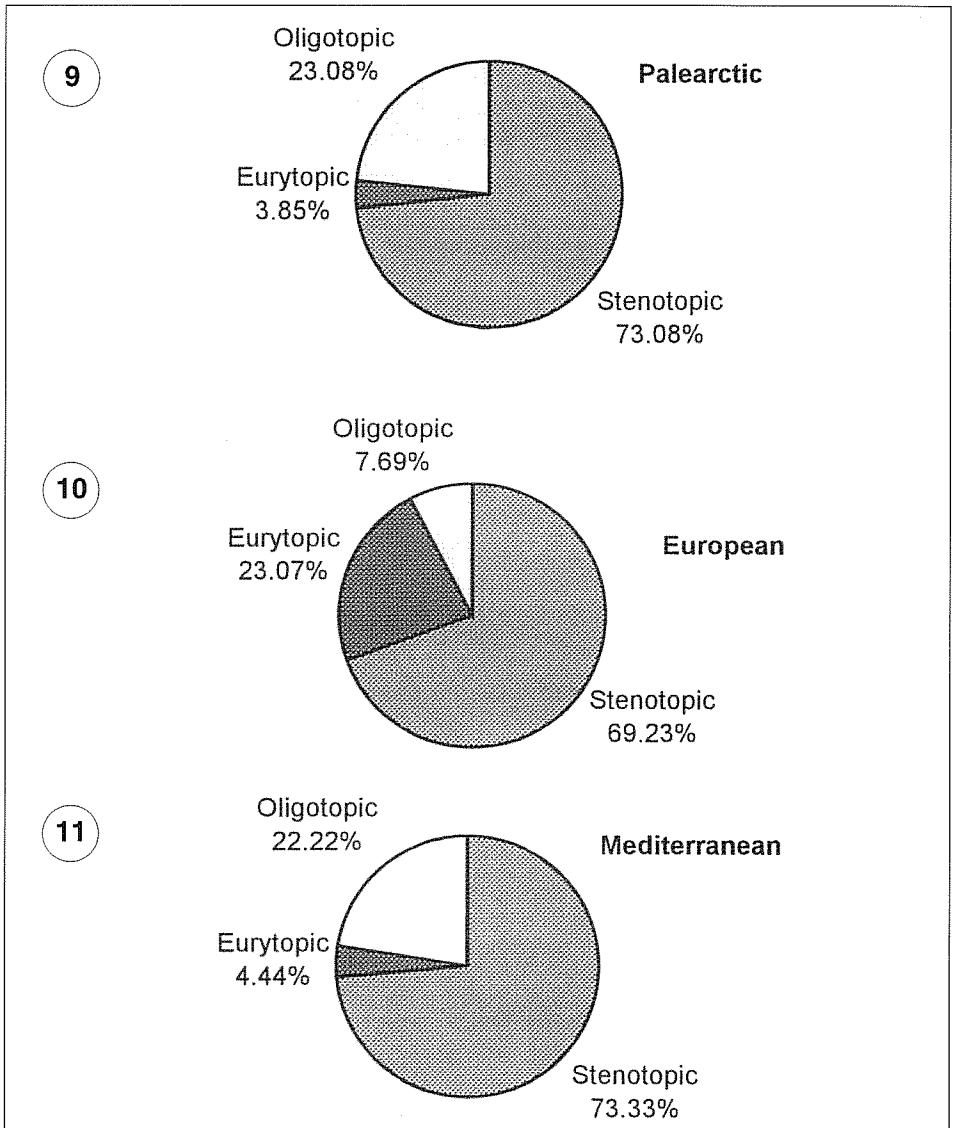


Fig. 8 - Zoogeographic spectrum of tenebrionid beetles

$\chi^2 = 32.001$ ($df = 2$, $p < 0.001$) for the European species and $\chi^2 = 34.533$ ($df = 2$, $p < 0.001$) for the Mediterranean+Afrotropical species. In particular, the stenotopic species were represented with higher proportions in all of these distribution types. The oligotopic species were an important component of the species widely distributed in the Palearctic region, while the eurytopic species were highly represented among the species distributed in Europe.

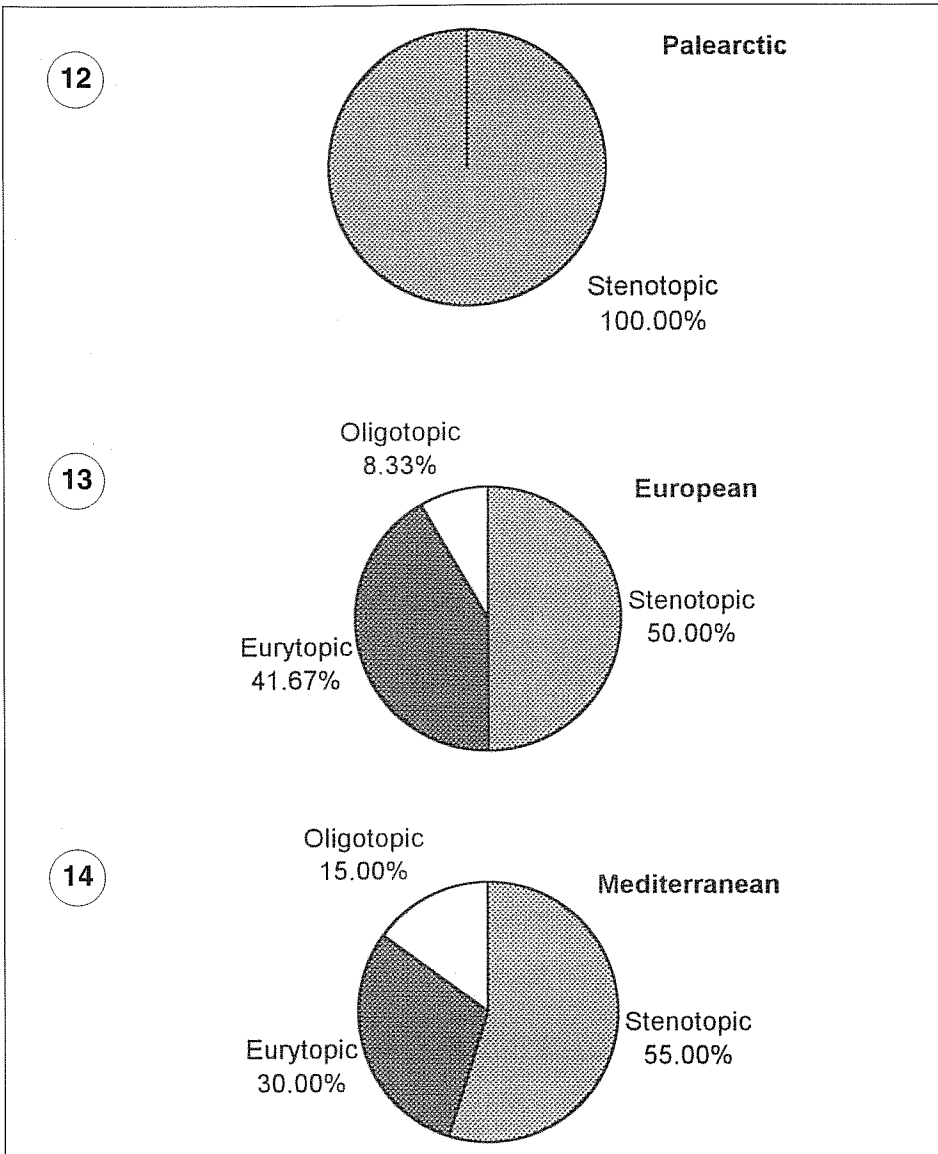
As to the tenebrionids, the distribution of steno-, oligo- and eurytopic species did not significantly differ from a uniform distribution in the different distribution types, the χ^2 values being $\chi^2 = 0.091$ ($df = 1$, $p = 0.763$) for the European species (with the only one oligotopic species omitted to have expected frequencies > 5) and $\chi^2 = 4.900$ ($df = 2$, $p = 0.086$) for the Mediterranean species. However, the stenotopic species were represented with higher proportions in all of these distributional types, being 100% of the Palearctic ones. The oligotopic species were poorly represented, while the eurytopic species were



Figs. 9-11 - Proportion of steno-, oligo- and eurytopic carabid species in each zoogeographic category

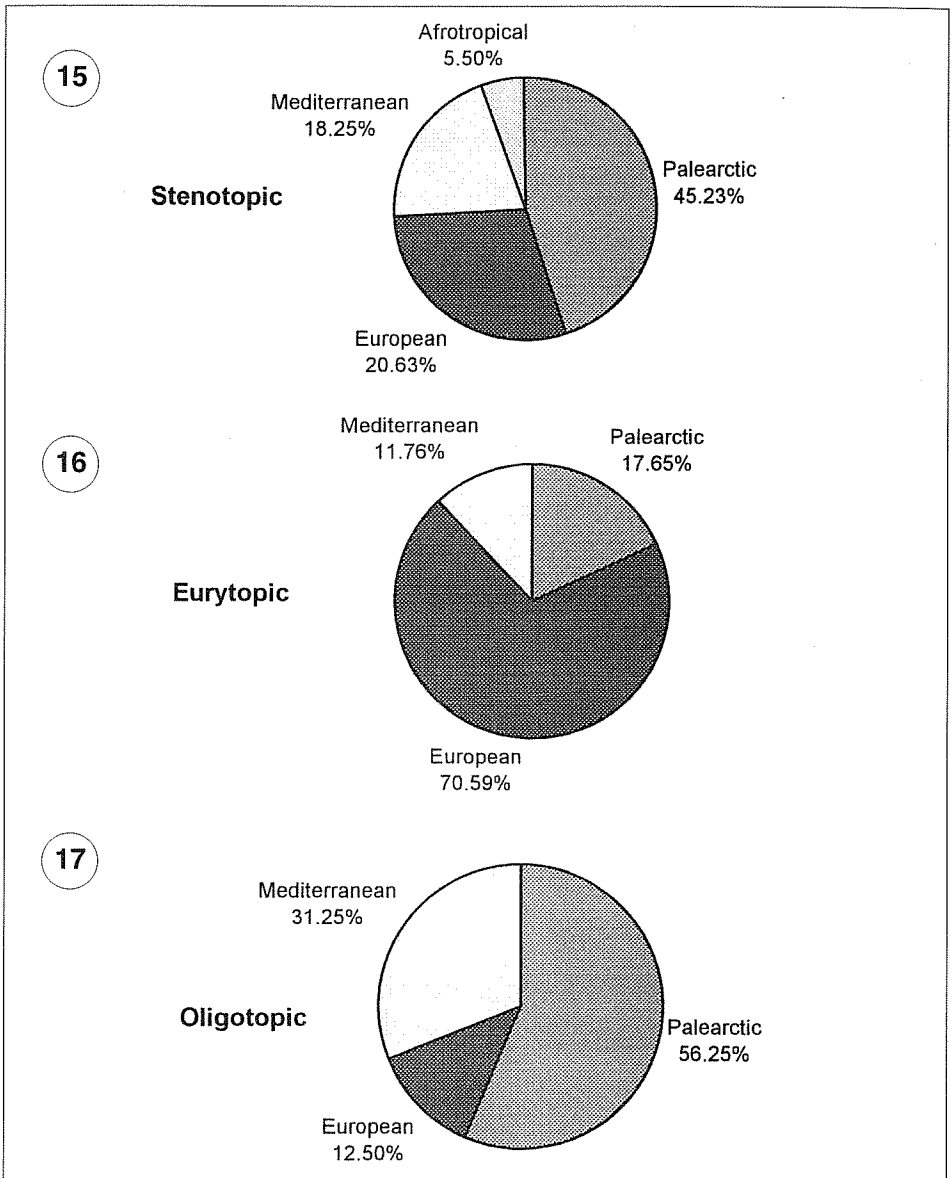
highly represented among the species distributed in Europe and in the Mediterranean.

Figs. 15-20 show the proportion the general distribution types among the stenotopic, oligotopic and eurytopic species in the two families. For the carabid beetles, the stenotopic species were mostly represented by species widely distributed in the Palearctic region, followed by the species distributed in Europe



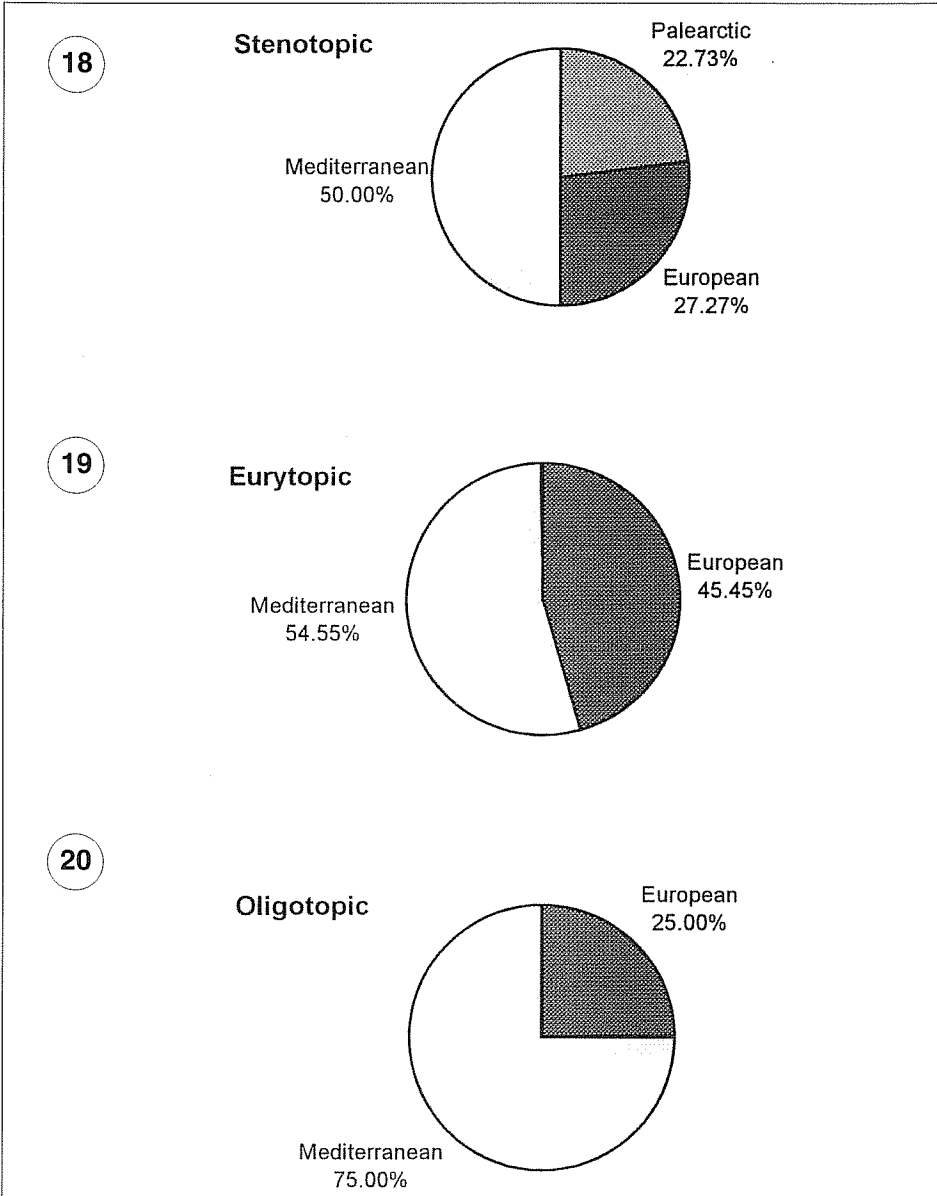
Figs. 12-14 - Proportion of steno-, oligo- and eurytopic tenebrionid species in each zoogeographic category

and by those distributed in the Mediterranean ($\chi^2 = 8.143$, $df = 2$, $p = 0.017$). The eurytopic species were mostly represented by species distributed in Europe ($\chi^2 = 10.707$, $df = 2$, $p = 0.005$), while the oligotopic species were greatly represented by species distributed in the Paelearctic region and in the Mediterranean ($\chi^2 = 9.250$, $df = 2$, $p = 0.010$). In all cases, χ^2 tests were significant.



Figs. 15-17 - Proportion of each zoogeographic category in each ecological category for carabid beetles

As to the tenebrionid beetles, the stenotopic species were mostly represented by species distributed in the Mediterranean region, followed by the species distributed in Europe and by those distributed in the Palearctic region, but differences were not significant ($\chi^2 = 2.818$, $df = 2$, $p = 0.244$). The oligotopic



Figs. 18-20 - Proportion of each zoogeographic category in each ecological category for tenebrionid beetles

species were mostly represented by species distributed in the Mediterranean (χ^2 inapplicable due to expected frequencies < 5). Finally, the eurytopic species were represented by species distributed in the Mediterranean and in Europe with similar frequencies ($\chi^2 = 0.091$, $df = 1$, $p = 0.763$).

DISCUSSION

Both carabid and tenebrionid beetles were highly speciose in the study area. However, their distribution in the different habitats was very different. Carabids were richest in wetlands and in open areas, while tenebrionids on the dune and in the natural forest habitat.

This can be related to the very different general ecology of the two families. Carabids are typically geophilous and hygrophilous beetles, thus being speciose in wetlands and open areas with ponds, but poorly represented in dry areas, where they occur with few highly specialised species. By contrast, tenebrionids are generally more thermophilous beetles, including psammophilous, geophilous and xylophilous species. Thus, two main thermophilous guilds can be recognised for tenebrionids: (1) species associated with the dune; and (2) species associated with the oak forest (see Fattorini and Maltzëff, 2001).

The high proportion of stenotopic species in carabids is also due to their hygrophilous preferences, being most species strictly associated with only one habitat type: the wetlands or the open habitats occupied by ponds.

The high number of stenotopic species makes high the beta-diversity of this family within the study area. In particular, as the wetlands are occupied by a high proportion of stenotopic species, this concentration of species restricted to one habitat strongly increases the extent of species replacement among habitats.

By contrast, tenebrionids are generally more widely distributed in the study area, showing a lower value of beta-diversity. In fact, the psammophilous species, which represent a relevant part of the tenebrionid fauna, are generally considered as stenoecious species, but, as there are several sandy habitats in the study area, some of them occupy more than one habitat, being thus classified as oligo- or eurytopic species. Therefore, the occurrence, in the study area, of several habitats suitable for such species, allow these insects to have a local high habitat breadth. However, the stenotopic species actually form a relevant percentage of the fauna associated with the dune. The high percentages of stenotopic species in natural forest, wetlands and oak forest depend on the presence of xylophilous species linked to particular plant associations. Finally, the low percentage of stenotopic species (one species) in open areas is related to the fact that the tenebrionids of open areas are typically geophilous or psammophilous species, also living in other habitats. This is an important difference: while carabids found in open areas are associated with ponds, the tenebrionids living in open areas are associated with steppes (see Fattorini and Maltzëff, 2001; Vigna Taglianti et al., 2001). The two families thus exploit two micro-habitats within the same major habitat, the carabids being dependent on ponds, the tenebrionid on dry soils.

The high incidence of hygrophilous species among carabids (see Vigna Taglianti et al., 2001) – a common feature of carabid faunas (e.g., hydrophiles *sensu* Darlington, 1971; Casale and Vigna Taglianti, 1999) - can explain the

observed zoogeographic spectrum. As a rule, we can admit that as carabids generally include many hygrophilous species, this family can be very speciose in the study area, where wetlands and ponds are greatly available. Also, as the hygrophilous species are typically widely distributed in the Palearctic region (while Mediterranean elements are generally more xero-thermophilous) (cf. Tab. I), the high percentage of species distributed in Europe and in the Palearctic region can be explained by these ecological preferences. As the stenotopic species are mostly represented by 'Palearctic species', and the stenotopic species are represented with high percentage in the study area, it is obvious that the 'Palearctic species' are the most important in the zoogeographic spectrum. This apparently circular reasoning cannot however be extended to the other ecological categories. The stenotopic species are very abundant among the 'Palearctic species', as expected by the fact that these two categories are the most abundant, but they are also the most abundant in all other types of geographical distributions. This may suggest that a hygrophilic character is probably shown by most of the species belonging to all the chorotypes. Even if 'stenotopic' does not mean hygrophilous, the majority of stenotopic species are actually hygrophilous, being localised in wetlands and open areas occupied by ponds.

As to the tenebrionids, most of the species are distributed in the Mediterranean region, in accordance with the general thermophily shown by these beetles. Also, most of the species are stenotopic. However, the two facts (high proportion of 'Mediterranean species' and high proportion of stenotopic species) do not appear strictly related. In fact, the stenotopic species include also many species distributed in the Palearctic region or at least in Europe. Also, the species distributed in the Mediterranean include a high proportion of eurytopic species. This can be explained by the fact that, in contrast with carabids (where stenotopic species are nearly all hygrophilous), stenotopic tenebrionids include at least two categories: stenotopic species associated with sandy soils, and stenotopic species associated with trees.

CONCLUSIONS

Both present (environmental) and historical (paleoecological) factors can be evoked to explain the species richness, beta-diversity, habitat distribution and zoogeographic spectrum of the carabid and tenebrionid beetles in the study area.

Past climates have oscillated greatly from the Eocene to post Pleistocene with some periods, such as Pleistocene glacials, being relatively cool and others being warmer or dryer in both North America and Europe. Such large-scale climatic fluctuations forced insect populations to change their geographical distribution (e.g., Noonan, 1988; Reimann et al., 2002). The glacial periods forced more vagile insects southward, with many of these subsequently expanding northward in post-glacial times. Many groups of extant insects have species extending into or even

endemic to regions covered by ice during Pleistocene glacials, and formerly glaciated areas now have a rich insect fauna. Dispersal with accompanying changes in range can be the only explanation for presence in such areas (Noonan, 1988 and references therein). Within this general pattern, two opposite types of range changes should be however distinguished according to the ecology of the involved species (see Reimann et al., 2002 and references therein). During cold periods, species adapted to warm-temperate climates actually retreated into southern localised refugia (mainly situated on the large European peninsulas and the Balkans), while cold-adapted species were favoured in expanding their range in central and southern Europe. By contrast, during warm periods, species adapted to temperate-warm climatic conditions expanded over large distances to central and even northern Europe, whereas cold-adapted species were driven away to the High North and to the high altitudes (see Reimann et al., 2002 and references therein).

Both carabids and tenebrionids recorded in the coastal area of Castelporziano conform to these two opposite general patterns. However, carabids conform especially to the pattern of cold-adapted species, while tenebrionids to that of temperate-warm adapted species.

From an ecological point of view, the occurrence of many carabid species with 'Palearctic' chorotypes (which are also typically stenotopic hygrophilous species) can be related to the presence of wetlands and ponds, which appear the most diversified habitats. Most probably, such species largely colonised Italian coastal areas during Pleistocene glaciations, as a consequence of a colder climate that favoured the dispersal of mesophilous species from northern and inland regions to southern and coastal areas. As the climate became drier and warmer, these species were forced to assume more northern distributions. However, isolated populations were able to survive also in areas where favourable habitats (e.g., wetlands with mesophilous vegetation) persisted. Therefore, these relict populations are a result of vicariance events determined by the fragmentation of mesophilous habitats widespread during Pleistocene glaciations (cf. Blondel and Aronson, 1999).

The occurrence of many thermophilous species with 'Mediterranean' chorotypes among the tenebrionids (as well as the presence of some Mediterranean carabids) can be related to the Mediterranean feature of the area and to the hypothetical refugial role of the Tyrrhenian coasts during Pleistocene glaciations. In fact, the interior portions of continents were generally colder than places nearer the coasts, which could have operated as refugia thanks to their more temperate climate, especially along the seashore (cf. Noonan, 1988; Cruzan and Templeton, 2000).

In accordance with the Tyrrhenian location of the study area, a great number of species appear to be more or less widely distributed in the Mediterranean basin; obviously, species with such type of distribution are also typically thermophilous species. Therefore, the climate of the study area, favouring

species with thermophilous preferences, can be responsible for a high incidence of species with such ranges and for the high number of species recorded for the dune and the oak forest. The present occurrence of some species with 'northern' chorotypes can be related to the presence, in the study area, of hygrophilous/mesophilous phytocoenoses. As discussed for the carabid beetles, xylophilous tenebrionid species, associated with mesophilous phytocoenoses, probably colonised the coastal areas during glaciations, and, when the climate became drier and warmer, were forced to assume more northern distributions, leaving isolated populations in coastal areas where favourable habitats persisted.

To conclude, the carabid and tenebrionid beetles presently occurring in the study area experienced the same historical events, but responded very differently according to their ecology, thus showing the importance of a thorough knowledge of the general ecological preferences of animal groups in postulating historical models. Most of the carabid fauna is composed of species that shifted their range southwards during the glacials, being represented by species widely distributed in the Palearctic region and associated with wetlands. Tenebrionids, which are typically thermophilous, are speciose especially in the dry habitats, and are mostly represented by species distributed in the Mediterranean, which, during the glacials, found refuges in coastal areas. However, even in this family, glacial colonisation by 'northern' elements, which found suitable wet habitats, enriched the fauna with stenoecious species typically associated with wetlands and mesophilous forests. Thus, during the glacials, the same area operated as a refugium for thermophilous species (most of the tenebrionids), but was also colonised by cold-adapted species (most of the carabids). These hypotheses are based on eco-geographical evidences and need to be supported by other data. Procedures based on genetic information (e.g., Cruzan and Templeton, 2000; Jorgensen, 2000; Reimann et al., 2002) could be applied to test the models discussed in this paper.

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Tab. I - Carabid beetles collected in the study area

| | Corotype | Ecological category | BE | DU | LM | HM | WE | OF | MF | OA |
|----|--------------------------------------|---------------------|----|----|----|----|----|----|----|----|
| 1 | <i>Cicindela campestris</i> | PAL | S | | | | | | | + |
| 2 | <i>Myriochile melancholica</i> | AIM | S | | | | + | | | |
| 3 | <i>Lophyridia littoralis</i> | CEM | O | + | + | | | | | |
| 4 | <i>Calosoma inquisitor</i> | SIE | S | | | | | | + | |
| 5 | <i>Calosoma sycophanta</i> | PAL | S | | | | | | + | |
| 6 | <i>Campalita maderae</i> | MED | S | | | | | | | + |
| 7 | <i>Carabus granulatus</i> | ASE | O | | + | | + | | | |
| 8 | <i>Carabus italicus</i> | SEU | S | | | | + | | | |
| 9 | <i>Carabus alysidotus</i> | WME | O | | | | + | | | + |
| 10 | <i>Carabus rossii</i> | SEU | E | | | + | | | + | + |
| 11 | <i>Carabus convexus</i> | SIE | O | | | | + | | + | |
| 12 | <i>Carabus lefebvrei</i> | SEU | E | | | + | + | | + | |
| 13 | <i>Carabus coriaceus</i> | EUR | S | | | | | | | + |
| 14 | <i>Carabus violaceus</i> | EUR | O | | | | | | + | + |
| 15 | <i>Cychnus italicus</i> | SEU | S | | | | | | + | |
| 16 | <i>Leistus fulvibarbis</i> | EUM | S | | | | + | | | |
| 17 | <i>Eurynebria complanata</i> | WME | S | + | | | | | | |
| 18 | <i>Nebria brevicollis</i> | TUE | S | | | | + | | | |
| 19 | <i>Notiophilus rufipes</i> | EUR | E | | | + | + | + | + | |
| 20 | <i>Notiophilus geminatus</i> | MED | S | | | | | | + | |
| 21 | <i>Notiophilus substriatus</i> | EUR | E | + | + | | + | | + | |
| 22 | <i>Omophron limbatum</i> | PAL | S | | | | + | | | |
| 23 | <i>Elaphrus uliginosus</i> | ASE | S | | | | + | | | |
| 24 | <i>Siagona europaea</i> | AIM | S | | | | | | | + |
| 25 | <i>Distichus planus</i> | AIM | S | | | | + | | | |
| 26 | <i>Scarites buparius</i> | MED | S | + | | | | | | |
| 27 | <i>Clivina fossor</i> | ASE | O | | | | + | | | + |
| 28 | <i>Dyschiriodes globosus</i> | SIE | S | | | | + | | | |
| 29 | <i>Dyschiriodes chalybaeus</i> | MED | S | | | | + | | | |
| 30 | <i>Asaphidion curtum</i> | WME | S | | | | + | | | |
| 31 | <i>Asaphidion stierlini</i> | MED | S | | | | + | | | |
| 32 | <i>Metallina ambigua</i> | WME | S | | | | + | | | |
| 33 | <i>Metallina lampros</i> | PAL | O | | | | + | | | + |
| 34 | <i>Phyla tethys</i> | MED | S | | | | + | | | |
| 35 | <i>Leja assimilis</i> | WPA | S | | | | + | | | |
| 36 | <i>Leja articulata</i> | ASE | S | | | | + | | | |
| 37 | <i>Leja octomaculata</i> | PAL | S | | | | + | | | |
| 38 | <i>Philochthus inoptatus</i> | SEU | S | | | | + | | | |
| 39 | <i>Philochthus escherichi</i> | MED | S | | | | + | | | |
| 40 | <i>Philochthus lunulatus</i> | EUM | S | | | | + | | | |
| 41 | <i>Ocydromus latinus</i> | SEU | S | | | | + | | | |
| 42 | <i>Ocydromus tetragrammus</i> | EUM | S | | | | + | | | |
| 43 | <i>Ocydromus callosus</i> | MED | S | | | | + | | | |
| 44 | <i>Synechostictus dabli</i> | WME | S | | | | + | | | |
| 45 | <i>Synechostictus elongatus</i> | SEU | S | | | | + | | | |
| 46 | <i>Ocys harpaloides</i> | EUM | S | | | | + | | | |
| 47 | <i>Paratachys bistriatus</i> | WPA | S | | | | + | | | |
| 48 | <i>Paratachys fulvicollis</i> | TUE | S | | | | + | | | |
| 49 | <i>Sphaerotachys hoemorrhoidalis</i> | AFM | S | | | | + | | | |
| 50 | <i>Tachyta nana</i> | OLA | S | | | | + | | | |
| 51 | <i>Trechus quadristriatus</i> | TEM | E | | | + | + | | | + |
| 52 | <i>Trechus fairmairei</i> | SEU | S | | | | + | | | |
| 53 | <i>Paranchus albipes</i> | EUM | S | | | | + | | | |

| | | | | | | | | | | | | |
|-----|-----------------------------------|-----|---|--|--|---|---|---|---|---|---|---|
| 54 | <i>Anchomenus dorsalis</i> | PAL | S | | | | | | | + | | |
| 55 | <i>Agonum marginatum</i> | WPA | S | | | | | | | + | | |
| 56 | <i>Agonum viridicupreum</i> | TUE | S | | | | | | | + | | |
| 57 | <i>Agonum permolestum</i> | SEU | S | | | | | | | + | | |
| 58 | <i>Agonum nigrum</i> | TEM | S | | | | | | | + | | |
| 59 | <i>Agonum sordidum</i> | EME | S | | | | | | | + | | |
| 60 | <i>Olisthopus fuscatus</i> | MED | O | | | + | | | | | | + |
| 61 | <i>Olisthopus glabricollis</i> | EME | O | | | + | | | | | | + |
| 62 | <i>Platyderus neapolitanus</i> | SEU | E | | | + | | + | + | + | + | |
| 63 | <i>Synuchus vivalis</i> | ASE | O | | | | | | | + | + | |
| 64 | <i>Calathus circumseptus</i> | WME | O | | | | | | + | | | + |
| 65 | <i>Calathus cinctus</i> | WPA | E | | | + | | | | | + | + |
| 66 | <i>Calathus montivagus</i> | SEU | E | | | + | + | | | | + | |
| 67 | <i>Calathus fuscipes</i> | EUM | E | | | + | | | | | + | + |
| 68 | <i>Laemostenus venustus</i> | EME | O | | | | | | | + | + | |
| 69 | <i>Laemostenus latialis</i> | WME | S | | | | | | | | + | |
| 70 | <i>Laemostenus algerinus</i> | WME | E | | | + | + | | | | | |
| 71 | <i>Platysma nigrum</i> | ASE | S | | | | | | | + | | |
| 72 | <i>Platysma nigrita</i> | PAL | S | | | | | | | + | | |
| 73 | <i>Platysma anthracinum</i> | CAE | S | | | | | | | + | | |
| 74 | <i>Platysma gracile</i> | ASE | S | | | | | | | + | | |
| 75 | <i>Platysma oenotrium</i> | SEU | S | | | | | | | + | | |
| 76 | <i>Platysma macrum</i> | ASE | S | | | | | | | | | + |
| 77 | <i>Steropus melas</i> | EUR | E | | | + | | | | | + | + |
| 78 | <i>Pterostichus micans</i> | SEU | S | | | | | | | | + | |
| 79 | <i>Argutor cursor</i> | SEU | S | | | | | | | + | | |
| 80 | <i>Argutor vernalis</i> | PAL | S | | | | | | | + | | |
| 81 | <i>Phonias strenuus</i> | ASE | S | | | | | | | + | | |
| 82 | <i>Omasseus aterrimus</i> | WPA | S | | | | | | | + | | |
| 83 | <i>Poecilus cupreus</i> | ASE | O | | | | | | | + | | + |
| 84 | <i>Poecilus koyi</i> | SIE | S | | | | | | | | | + |
| 85 | <i>Abax ater</i> | EUR | O | | | | | | | + | | + |
| 86 | <i>Zabrus tenebrioides</i> | TUE | S | | | | | | | | | + |
| 87 | <i>Amara concinna</i> | EUR | S | | | | | | | + | | |
| 88 | <i>Amara aenea</i> | PAL | O | | | | | | | | + | + |
| 89 | <i>Amara anthobia</i> | EUR | S | | | | | | | + | | |
| 90 | <i>Amara apricaria</i> | PAL | S | | | | | | | | | + |
| 91 | <i>Scybalicus oblongiusculus</i> | MED | S | | | | | | | | | + |
| 92 | <i>Anisodactylus binotatus</i> | ASE | S | | | | | | | + | | |
| 93 | <i>Gynandromorphus etruscus</i> | SEU | S | | | | | | | | | + |
| 94 | <i>Diachromus germanus</i> | TEM | S | | | | | | | | | + |
| 95 | <i>Carterus dama</i> | MED | S | | | | | | | | | + |
| 96 | <i>Ditomus calydonius</i> | TUE | S | | | | | | | | | + |
| 97 | <i>Acinopus picipes</i> | TUE | S | | | | | | | | | + |
| 98 | <i>Parophonus maculicornis</i> | SEU | S | | | | | | | | | + |
| 99 | <i>Parophonus hispanus</i> | WME | S | | | | | | | | | + |
| 100 | <i>Parophonus mendax</i> | SEU | S | | | | | | | | | + |
| 101 | <i>Ophonus sabulicola</i> | TUE | S | | | | | | | | | + |
| 102 | <i>Ophonus ardosiacus</i> | EUM | S | | | | | | | | | + |
| 103 | <i>Ophonus azureus</i> | CEM | S | | | | | | | | | + |
| 104 | <i>Ophonus puncticeps</i> | TUE | S | | | | | | | | | + |
| 105 | <i>Ophonus schaubergerianus</i> | EUR | S | | | | | | | | | + |
| 106 | <i>Ophonus incisus</i> | MED | S | | | | | | | | | + |
| 107 | <i>Cryptophonus melancholicus</i> | EUM | S | | | | | | | + | | |
| 108 | <i>Cryptophonus tenebrosus</i> | WPA | S | | | | | | | | | + |
| 109 | <i>Pseudophonus griseus</i> | PAL | S | | | | | | | | | + |
| 110 | <i>Pseudophonus rufipes</i> | PAL | O | | | | | | | + | | + |
| 111 | <i>Harpalus distinguendus</i> | PAL | O | | | | | | | + | | + |
| 112 | <i>Harpalus oblitus</i> | TEM | O | | | | | | | + | | + |

| | | | | | | | | | |
|-----|-------------------------------------|-----|---|---|---|---|---|---|---|
| 113 | <i>Harpalus smaragdinus</i> | ASE | S | | | | | | + |
| 114 | <i>Harpalus cupreus</i> | SEU | S | | | + | | | |
| 115 | <i>Harpalus pygmaeus</i> | SEU | S | | | | | | + |
| 116 | <i>Harpalus dimidiatus</i> | EUR | O | | | + | | | + |
| 117 | <i>Harpalus rubripes</i> | ASE | O | + | | | | | + |
| 118 | <i>Harpalus attenuatus</i> | MED | O | | + | | | | + |
| 119 | <i>Harpalus sulphuripes</i> | EUM | E | + | | + | | | + |
| 120 | <i>Harpalus serripes</i> | PAL | S | | | | | | + |
| 121 | <i>Harpalus tardus</i> | ASE | O | | | + | | + | |
| 122 | <i>Harpalus anxius</i> | PAL | O | | | + | | | + |
| 123 | <i>Stenolophus teutonius</i> | TEM | S | | | + | | | |
| 124 | <i>Stenolophus persicus</i> | EME | S | | | + | | | |
| 125 | <i>Stenolophus skrimsbiranus</i> | EUM | S | | | + | | | |
| 126 | <i>Stenolophus mixtus</i> | PAL | S | | | + | | | |
| 127 | <i>Bradycellus verbasci</i> | TUE | O | + | | + | | | |
| 128 | <i>Acupalpus meridianus</i> | EUR | S | | | + | | | |
| 129 | <i>Acupalpus elegans</i> | TEM | S | | | + | | | |
| 130 | <i>Acupalpus parvulus</i> | ASE | S | | | + | | | |
| 131 | <i>Acupalpus maculatus</i> | EUM | S | | | + | | | |
| 132 | <i>Acupalpus notatus</i> | MED | S | | | + | | | |
| 133 | <i>Acupalpus paludicola</i> | MED | S | | | + | | | |
| 134 | <i>Acupalpus luteatus</i> | SIE | S | | | + | | | |
| 135 | <i>Acupalpus brunnipes</i> | EUM | S | | | + | | | |
| 136 | <i>Anthracus quarmerensis</i> | SEU | S | | | + | | | |
| 137 | <i>Anthracus transversalis</i> | EUR | S | | | + | | | |
| 138 | <i>Licinus silphoides</i> | SEU | S | | | | | | + |
| 139 | <i>Badister meridionalis</i> | SEU | S | | | + | | | |
| 140 | <i>Badister dilatatus</i> | SIE | S | | | + | | | |
| 141 | <i>Panagaeus cruxmajor</i> | SIE | S | | | + | | | |
| 142 | <i>Epomis circumscriptus</i> | AFM | S | | | + | | | |
| 143 | <i>Epomis dejeani</i> | EME | S | | | + | | | |
| 144 | <i>Chlaenius spoliatus</i> | PAL | S | | | + | | | |
| 145 | <i>Chlaenius festivus</i> | TUE | S | | | + | | | |
| 146 | <i>Chlaenius chrysocephalus</i> | WME | O | | | + | | | + |
| 147 | <i>Dinodes decipiens</i> | EUM | S | | | | | | + |
| 148 | <i>Chlaeniellus vestitus</i> | PAL | S | | | + | | | |
| 149 | <i>Chlaeniellus nigricornis</i> | ASE | S | | | + | | | |
| 150 | <i>Chlaeniellus nitidulus</i> | CAE | S | | | + | | | |
| 151 | <i>Chlaeniellus olivieri</i> | SEU | S | | | + | | | |
| 152 | <i>Chlaeniellus tristis</i> | PAL | S | | | + | | | |
| 153 | <i>Oodes belopioides</i> | SIE | S | | | + | | | |
| 154 | <i>Lamprias fulvicollis</i> | WME | S | | | | | | + |
| 155 | <i>Lebia scapularis</i> | CEM | S | | | | | | + |
| 156 | <i>Demetrius atricapillus</i> | EUM | E | + | + | + | | | |
| 157 | <i>Pseudomasoreus canigoulensis</i> | WME | O | | | + | | + | |
| 158 | <i>Paradromius linearis</i> | EUM | E | + | + | + | | | |
| 159 | <i>Dromius meridionalis</i> | SIE | O | | | + | | + | |
| 160 | <i>Philorhizus melanocephalus</i> | TEM | E | | + | | + | + | |
| 161 | <i>Philorhizus crucifer</i> | MED | S | | | | | + | |
| 162 | <i>Syntomus impressus</i> | MED | E | | + | | | + | + |
| 163 | <i>Syntomus obscuroguttatus</i> | EUM | E | + | | + | | + | |
| 164 | <i>Microlestes corticalis</i> | TUM | S | | | | | | + |
| 165 | <i>Microlestes fulvibasis</i> | TUM | O | | + | | | | + |
| 166 | <i>Microlestes fissuralis</i> | TUE | S | | | | | | + |
| 167 | <i>Microlestes minutulus</i> | OLA | O | | | + | | | + |
| 168 | <i>Zuphium olens</i> | AIM | S | | | | | | + |
| 169 | <i>Drypta dentata</i> | AFP | S | | | + | | | |
| 170 | <i>Brachinus crepitans</i> | PAL | S | | | | | | + |
| 171 | <i>Brachinus ganglbaueri</i> | MED | O | | | + | | | + |

| | | | | |
|-------------------------------------|-----|---|---|---|
| 172 <i>Brachinus plagiatus</i> | MED | S | + | |
| 173 <i>Brachinus immaculicornis</i> | MED | O | + | + |
| 174 <i>Brachinus sclopeta</i> | EUM | O | + | + |
| 175 <i>Brachinus italicus</i> | WME | S | | + |

Chorotypes: OLA = Holarctic, PAL = Palearctic, WPA = W-Palearctic, ASE = Asiatic-European, SIE = Sibero-European, CEM = Centralasiatic-European-Mediterranean, CAE = Centralasiatic-European, TEM = Turano-European-Mediterranean, TUE = Turano-European, TUM = Turano-Mediterranean, EUM = Europeo-Mediterranean, EUR = European, SEU = S-European, MED = Mediterranean, WME = W-Mediterranean, EME = E-Mediterranean, AIM = Afrotropico-Indo-Mediterranean, AFM = Afrotropico-Mediterranean, AFP = Afrotropical + Palearctic. Ecological categories: E = Eurytopic, O = Oligotopic, S = Stenotopic. BE = Beach, DU = Dunes, LM = Low maquis; HM = High maquis, WE = Wetlands, OF = Oak forest, MF = Mesophilous forest, OA = Open areas. Nomenclature follows Vigna Taglianti et al. (2001).

Tab. II - Tenebrionid beetles collected in the study area

| | Corotype | Ecological category | BE | DU | LM | HM | WE | OF | MF | OA |
|------------------------------------|----------|---------------------|----|----|----|----|----|----|----|----|
| 1 <i>Erodius siculus</i> | EME | E | | + | + | | | | | + |
| 2 <i>Tentyria grossa</i> | WME | O | | + | + | | | | | |
| 3 <i>Stenosis intermedia</i> | SEU | S | | + | | | | | | |
| 4 <i>Stenosis sardoia</i> | WME | E | | | | + | + | + | + | + |
| 5 <i>Asida lugionii</i> | WME | E | | | + | + | | | | + |
| 6 <i>Scaurus striatus</i> | WME | E | | | + | + | | | | + |
| 7 <i>Pimelia bipunctata</i> | WME | E | | + | + | + | | | | + |
| 8 <i>Blaps gibba</i> | SEU | S | | | | | + | | | |
| 9 <i>Pedinus meridianus</i> | SEU | E | | | | | | + | | + |
| 10 <i>Colpotus strigosus</i> | SEU | E | | | | | | + | + | + |
| 11 <i>Dendarus lugens</i> | WME | S | | | | | | | | + |
| 12 <i>Gonocephalum granulatum</i> | TEM | S | | + | | | | | | |
| 13 <i>Ammobius rufus</i> | MED | S | | + | | | | | | |
| 14 <i>Trachyscelis aphodioides</i> | MED | S | | + | | | | | | |
| 15 <i>Phaleria acuminata</i> | MED | O | + | + | | | | | | |
| 16 <i>Phaleria provincialis</i> | MED | O | + | + | | | | | | |
| 17 <i>Halammobia pellucida</i> | MED | S | | + | | | | | | |
| 18 <i>Pseudoseriscus normandi</i> | WME | S | | + | | | | | | |
| 19 <i>Bolitophagus reticulatus</i> | SIE | S | | | | | + | | | |
| 20 <i>Diaperis boleti</i> | SIE | S | | | | | + | | | |
| 21 <i>Platydemus violaceum</i> | SEU | S | | | | | + | | | |
| 22 <i>Uloma culinaris</i> | SIE | S | | | | | + | | | |
| 23 <i>Diaclina testudinea</i> | SEU | S | | | | | | | + | |
| 24 <i>Hypophloeus unicolor</i> | EUR | S | | | | | | | + | |
| 25 <i>Iphthiminius italicus</i> | EME | S | | | | | | | + | |
| 26 <i>Menephilus cylindricus</i> | SEU | O | | | | | + | | + | |
| 27 <i>Tenebrio obscurus</i> | COS | S | | | | | | | + | |
| 28 <i>Neatus noctovagus</i> | EME | S | | | | | | | + | |
| 29 <i>Helops coeruleus</i> | EUR | E | | | | | + | + | + | |
| 30 <i>Gunarus parvulus</i> | WME | S | | + | | | | | + | |
| 31 <i>Catomus rotundicollis</i> | WME | E | | + | | | + | + | + | + |
| 32 <i>Enoplopus dentipes</i> | SEU | S | | | | | | | + | |
| 33 <i>Xanthomus pallidus</i> | WME | S | | + | | | | | | |
| 34 <i>Xanthomus pellucidus</i> | MED | S | | + | | | | | | |
| 35 <i>Nalassus aemulus</i> | WME | S | | + | | | | | | |
| 36 <i>Nalassus dryadophilus</i> | SEU | E | | | | | + | + | + | |
| 37 <i>Nalassus planipennis</i> | SEU | E | | | | | + | + | + | |

Acronyms as in Table I. Nomenclature follows Fattorini and Maltzeff (2001).