

Spatial Organisation of an Insect Ensemble in a Mediterranean Ecosystem: the Tenebrionid Beetles (Coleoptera: Tenebrionidae) Inhabiting an Adriatic Coastal Sand Dune Area

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Abstract: We studied the spatial organisation of an ensemble (phylogenetically bounded group of species that use a similar set of resources within a community) of tenebrionid beetles in a Mediterranean coastal sand dune ecosystem in Southern Italy (Molise region). Within a transect from the seashore to the inner dune, we identified four biotopes defined by different vegetation types. We found a community dominated by few sand-specialised and *r*-selected tenebrionid species. Overall tenebrionid abundance was lowest on the upper beach, highest on the embryonic shifting dunes and then from there declined further inland. The embryonic shifting dunes biotope showed the highest diversity and the lowest dominance. This pattern suggests that tenebrionid beetles are able to cope with the challenging salty and xerothermic conditions of the seaward margin. Although some species were too rare to assess their biotope preference, our data support that, at least some, were distributed with different abundance over the four dune biotopes. These differences are likely related to different preferences for different characteristics of substratum and detritus.

Key words: biotope, darkling beetles, dune vegetation, Habitat Directive, insect communities

Introduction

The Mediterranean beach-dune ecosystems are characterised by a relatively simple structure with a scarce and discontinuous vegetation cover (FEOLA *et al.* 2011). Because of soil drought and high summer temperatures, these ecosystems host a reduced number of insect species that are able to cope with such harsh conditions owing to their particular morphological, physiological and behavioural adaptations (FATTORINI 2008). Tenebrionid beetles (Coleoptera: Tenebrionidae) represent the most conspicuous component of the insect fauna inhabiting the Mediterranean beach-dune ecosystems in terms of species richness, abundance and biomass (COLOMBINI *et al.* 1991, FALLACI *et al.* 1994, FATTORINI 2008).

Tenebrionid communities of beach-dune ecosystems have been studied in various Mediterranean localities (see FATTORINI 2008 for a review). However, most of the available studies considered the “coastal” areas as single ecological units, without distinguishing the various types of biotopes (*sensu* DENNIS 2010) that occur from the sea-shore towards the inland. In fact, vegetational studies have clearly shown that, even along a distance of few meters from the seashore to the inner dunes there are different plant associations that reflect, on a spatial dimension, an ecological succession from the very pioneering plants that live close to the seashore to the more advanced plant communities of stabilised dunes (ACOSTA *et*

al. 2005). Previous studies have demonstrated that abundances of tenebrionid species differ from the sea-shore to the inner dune (COLOMBINI *et al.* 1994, FATTORINI *et al.* 2012, CARPANETO & FATTORINI 2001, 2003), thus suggesting that they may form distinct “ensembles”, i.e. phylogenetically bounded groups of species that use a similar set of resources within a community (FAUTH *et al.* 1996).

In general, research on insect assemblages has largely dealt with the study of the structure of the communities, i.e. groups of species that live in the same place at the same time, regardless of their ecological role. Insect guilds, i.e. groups of species that exploit the same class of environmental resources in a similar way (regardless of their taxonomic position), have been studied less frequently, because of difficulties in assessing how species really use the resources. The study of ensembles is considered even more difficult because the target species should belong to the same taxon, should be present in the same place at the same time, and should have a comparable ecology. These restrictions pose a number of practical problems, because it is difficult to sample simultaneously different biotopes that host species with comparable ecology and which are phylogenetically related.

The tenebrionid beetles of the Mediterranean beach-dune ecosystems represent an excellent study group for ensemble analyses, because (1) they are present in different, but related and easy to sample biotopes; (2) they belong to the same monophyletic group (family Tenebrionidae) and (3) they have similar ecology.

In this paper, we studied whether the ensemble of tenebrionid beetles inhabiting a Mediterranean coastal dune presents a spatial organisation associated with different biotopes defined by different plant associations.

Material and Methods

Study area and data collection

The Molise coast (Italy) extends for over 30 km along the Adriatic Sea. It is composed mainly of sandy beaches. The present study is focused on recent (Holocene) dunes included in a Site of Community Importance (SCI) called “Foce Saccione-Bonifica Ramitelli” (IT7222217) (FATTORINI *et al.* 2016). Sampling was done on a coastal sand dune system near Campomarino Town during spring and summer (June 2014, May 2015). Along the Adriatic shoreline, coastal dune systems are relatively low (less than 10 m height) and simple in structure (usually including only one dune ridge). They are character-

ised by a variety of distinct habitats: upper beach or drift line, embryo dunes, main dunes and fixed dunes (defining the inner margin of the Holocene dunes). At sites in good conservation state, such as the selected study area, coastal vegetation zonation follows a well recognisable sea-to-inland ecological gradient (ACOSTA *et al.* 2009).

On the basis of the dominant and diagnostic plant species indicated in the Habitat Directive Interpretation Manual (EU 2007), we identified four biotopes from the seashore to the inner dune (“EC habitats” – according to the coding scheme of the European Habitats Directive; European Commission 1992): 1210 Annual vegetation on drift lines; 2110 - Embryonic shifting dunes; 2120 - Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes); 2230 - *Malcolmieta* dune grasslands. This zonation reflects a natural stress gradient that develops along the sea-inland profile. For example, there is a decrease in wind speed and granulometry from the coast towards the inland, whereas humidity and detritus increase (CARBONI *et al.* 2001, FENU *et al.* 2013, ACOSTA *et al.* 2009). Along this gradient, both salinity and temperature tend to decrease (CHELAZZI *et al.* 1990).

Differences in these environmental parameters are responsible for the presence of biotopes typically disposed perpendicularly to the seashore. In the study area we recognised four biotopes corresponding to the four aforementioned European “habitats”. The biotope corresponding to the EC habitat 1210 was the closest to the seashore; it was located on the upper beach and was occupied by very sparse annual plant species. The biotope corresponding to the EC habitat 2110 has a denser vegetation cover, mostly represented by pioneer perennial plants such as *Elymus farctus*. The biotope corresponding to the EC habitat 2120 follows inland and corresponds to the main dune ridge, mainly defined by the presence of the dune-forming tussock grass, *Ammophila arenaria*. The biotope corresponding to EC habitat 2230 is the more inland biotope in the first part of the fixed dunes with many short annual grasses (ACOSTA *et al.* 2009).

In each year, each biotope was sampled using three square plots of 2×2 m placed at random along three transects separated by at least 100 m. Within each plot, beetles were collected by hand and by sieving a standard volume of sand. In order to reduce the risk that escaping animals abandoned the plot before being sampled, firstly we collected by hand all beetles that moved on the ground. Hand sampling was done by conscientiously searching for beetles on the ground, under leaves and at the base

of plants. Then, we collected a fixed volume of 12 litres of sand. This volume was collected by dividing the 2×2 m plot into four units of 1 m² and taking a sample of 3 litres of sand at the centre of each unit. Sand was collected by digging on a surface of about 400 cm² and down to a depth of 2-3 cm. We pooled data for each biotope because of the small number of species and individuals collected in each transect in the two years.

Data analysis

To test if the overall species abundance distribution matched the geometric series, which is typical of low-richness communities living in harsh environments and early successional stages (GILLER 1984, FATTORINI 2005, MCGILL *et al.* 2007), we used a rank-abundance curve approach (MAY 1975, MAGURRAN 1988, HAYEK & BUZAS 2010). We first tested with a χ^2 test if our data deviated significantly from the species abundance values predicted by this model. As our data did not deviate from the expected distribution, we used the Ordinary Least Squares (OLS) regression approach described by FATTORINI (2005) to model the rank-abundance curve. This approach is based on the fact that, if species are ranked from the most to the least abundant, and abundances are logarithmically transformed, a geometric series follows strictly a strength line that can be fitted using an OLS regression. The coefficient of determination R^2 can be used as a goodness-of-fit measure. The geometric series is the mathematical model used to express the “niche pre-emption” hypothesis, in which the sizes of the niche hypervolumes (measured by species relative abundances) are sequentially pre-empted from the most abundant to the least abundant species. The first species in the sequence occupies a fraction k of resource hypervolume, the second species a fraction k of hypervolume not occupied by the first, and so on. The niche pre-emption parameter k was calculated following HE & TANG (2008). We refrained from conducting biotope-specific analyses because of the small number of species recorded from each biotope.

Analysis of variance (ANOVA) was used to test if values of mean overall abundances of sampled tenebrionids were affected by biotope, transect or year. A χ^2 test was used to assess if overall abundances varied from a uniform (1:1:1:1) distribution among biotopes. To study if species distribution varied among biotopes (i.e. if species occurred with different proportional abundances in different biotopes), we used a species abundance × biotope contingency table. Then, we used separate χ^2 tests to assess variations from a uniform (1:1:1:1) distribution in the species abundance among biotopes.

Variations in the tenebrionid assemblages inhabiting the four biotopes were also studied by using the following indices of diversity, dominance and evenness (HAYEK & BUZAS 2010):

- Shannon-Wiener diversity index:

$$H' = -\sum \frac{n_i}{n} \ln \left(\frac{n_i}{n} \right), \quad \ln$$

where n_i is the abundance of species i and n is the overall abundance. H' ranges from 0 (one species dominates the community completely) to high values for communities with many species, each with few individuals;

- Simpson dominance index: $D = \sum \left(\frac{n_i}{n} \right)^2$. D

varies from 0 (all species are equally present) to 1 (one species dominates the assemblage completely);

- Margalef diversity index: $Mg = (S-1) / \ln(n)$, where S is the number of species;

- and Buzas and Gibson evenness index $E = e^{H'/S}$, where H' is the Shannon-Wiener index and S is the number of species.

Approximate confidence intervals for all indices were computed with a bootstrap procedure using PAST 3 (HAMMER *et al.* 2001). In each case, 9999 random samples were produced, each with the same total number of individuals as in the original sample. For each individual in the random sample, the taxon was chosen with probabilities proportional to the original abundances. Then a 95% confidence interval was calculated with $P < 0.05$ assumed to indicate a significant difference in a diversity index between the two samples.

Results

In total, we collected 116 individuals belonging to seven species (Fig. 1). The overall species abundance distribution did not deviate significantly from that expected according to the geometric series model with $k = 0.43$ ($\chi^2 = 6.13$, $df = 6$, $P = 0.190$). The equation of the OLS regression line was: $\log(A) = -0.25 \times \text{Rank} + 1.9$, with $R^2 = 0.950$ (Fig. 2). ANOVA results indicated that mean abundances did not differ among biotopes, because of the high variation in the number of sampled individuals among transects and years (Table 1, Fig. 3). Overall tenebrionid abundances deviated significantly from a uniform distribution among the four biotopes ($\chi^2 = 15.79$, $df = 3$, $P = 0.001$), which indicated that tenebrionids tend to concentrate in certain biotopes. Density attained the lowest value in the upper beach biotope (EC 1210), peaked in the EC 2110 biotope, and then decreased proceeding landwards.

Shannon-Wiener diversity (Fig. 4a) peaked in the biotope corresponding to EC 2110 ($H' = 1.60$), being significantly higher in this biotope than in those corresponding to EC 1210 ($H' = 0.79$, $P < 0.001$), EC 2120 ($H' = 0.97$, $P = 0.001$) and EC 2230 ($H' = 0.19$, $P < 0.001$). Shannon-Wiener index also showed a significant difference between the EC 2120 and EC 2230 biotopes ($P < 0.001$). Simpson dominance index (Fig. 4b) showed a parallel pattern, being significantly lower in the EC 2110 ($D = 0.23$) than in the EC 1210 ($D = 0.61$, $P < 0.001$), EC 2120 ($D = 0.41$, $P < 0.001$) and EC 2230 ($D = 0.90$, $P < 0.001$) biotopes. Simpson index also showed a significant difference between EC 2120 and EC 2230 ($P < 0.001$).

Margalef index (Fig. 4c) showed a pattern similar to that of Shannon-Wiener index, being significantly higher in EC 2110 ($Mg = 1.59$) than in the EC 2120 ($Mg = 0.57$, $P < 0.001$) and EC 2230 ($Mg = 0.33$, $P < 0.001$). No significant differences were found for evenness (Fig. 4d). Overall, diversity indices indicated that the four biotopes differed in their diversity, with the EC 2110 biotope having the highest diversity.

We found an association between species proportional abundances and biotopes ($\chi^2 = 58.45$, $df = 18$, $P < 0.0001$), which indicated that species occurred with different proportions in the four sampled biotopes (Fig. 1). *Ammobius rufus* (LUCAS, 1846) showed similar proportional abundances in the four biotopes ($\chi^2 = 3.20$, $df = 3$, $P = 0.36$), whereas the proportional abundance of *Pseudoseriscius helvolus* (KÜSTER, 1852) ($\chi^2 = 20.86$, $df = 3$, $P < 0.001$) and that of *Stenosis intermedia* (SOLIER, 1838) ($\chi^2 = 36.00$, $df = 3$, $P < 0.00001$) varied significantly among biotopes. Variations in the proportional abundance of *Pachychila frioli* SOLIER, 1835 was bordering on significance ($\chi^2 = 7.29$, $df = 3$, $P = 0.063$). The other species, namely *Erodium siculus* SOLIER, 1834, *Trachyscelis aphodioides* LATREILLE, 1809 and *Xanthomus pellucidus* MULSANT & REY, 1856, were not tested because of the small number of collected individuals (expected frequencies < 1).

Discussion

Tenebrionids living in Mediterranean beach-dune systems form relatively simple communities composed of few species, typically between six and 20 (FATTORINI 2008). Thus, the total species richness recorded in our study (7) falls within the range observed from other Italian sites. Moreover, the species recorded in Campomarino belong to the same genera found in other Italian dunes, including those

Table 1. ANOVA results for tenebrionid abundances in a beach-dune system in Southern Italy: df = degrees of freedom, SS = Type III sum of squares, MS = Mean square, F = F-ratio, P = probability level

	df	SS	MS	F	P
Biotope	3	76.333	25.444	1.713	0.202
Transect	2	54.333	27.167	1.829	0.191
Year	1	8.167	8.167	0.550	0.469
Error	17	252.500	14.853		

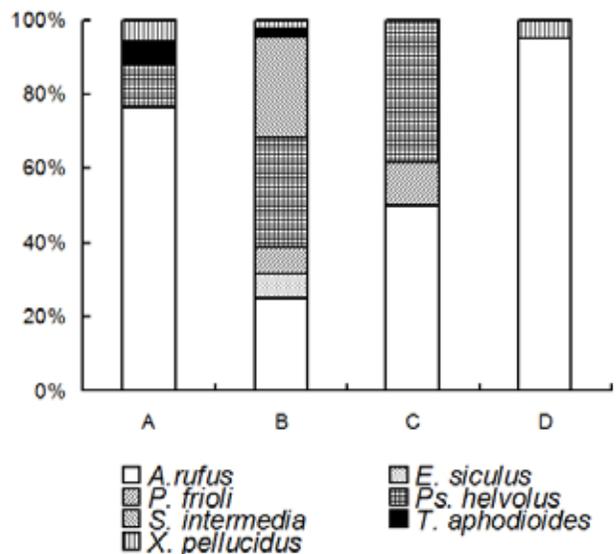


Fig. 1. Proportion of tenebrionid species in four biotopes along a beach-dune system in Southern Italy. A: Annual vegetation on drift lines; B: Embryonic shifting dunes; C: Shifting dunes along the shoreline with *Ammophila arenaria*; D: *Malcolmietalia* dune grasslands. Number of sampled individuals: $n = 17$ for A, $n = 44$ for B, $n = 34$ for C and $n = 21$ for D

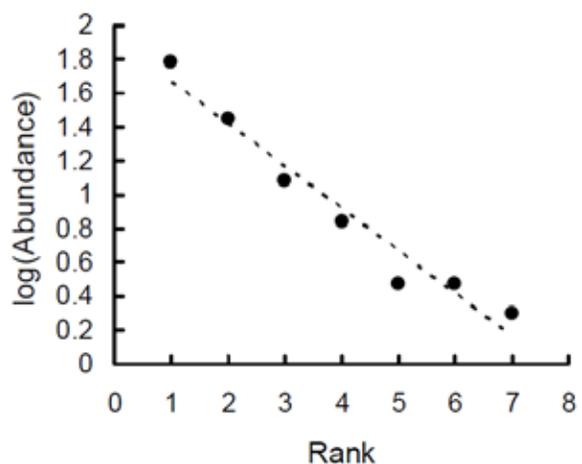


Fig. 2. Rank-abundance plot of the tenebrionid beetles inhabiting a beach-dune system in Southern Italy. Species are ranked from the most to the least abundant (x -axis). Species abundances are log-transformed (y -axis). Data were fitted using a linear regression (dashed line)

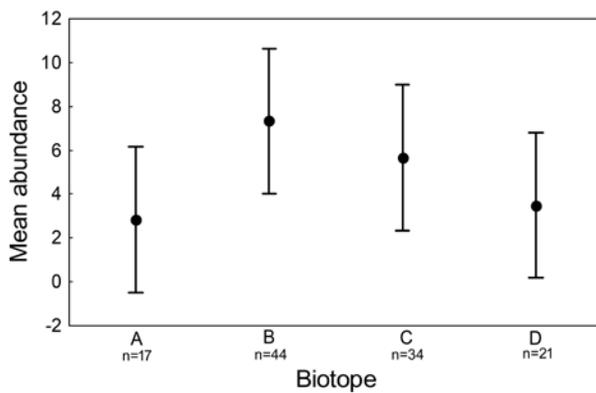


Fig. 3. Mean and overall tenebrionid abundance in the four studied biotopes. Dots represent mean abundances. Overall abundance is given as n below letters indicating biotopes. A: Annual vegetation on drift lines; B: Embryonic shifting dunes; C: Shifting dunes along the shoreline with *Ammophila arenaria*; D: *Malcolmietalia* dune grasslands. Vertical bars represent 95% confidence intervals

occurring in geographical regions that are very far from our study area (FATTORINI 2008). This can be related to the challenging environmental conditions of the Mediterranean dunes. Species that live in these arid environments have to be specialised to resist drought and high temperatures. As noted by DE LOS SANTOS (1994), only certain genera are able to colonise arid environments and exploit the limited resources which can be found there. This involves high morphological, behavioural and physiological specialisation, resulting in a low generic diversity. Thus, Mediterranean coastal areas can be relatively diversified in terms of species but most of them belong to few genera (i.e. *Erodius*, *Pimelia* or *Pachychila*) which are pre-adapted to arid environments, showing, e.g., dark colouring, greater elytral convexity, connected elytra and ticker chitin (see FATTORINI 2008).

The tenebrionid communities inhabiting sand dunes not only are composed of few species but also show a simple structure characterised by a high dominance of few species with large numbers of individuals (CARPANETO & FATTORINI 2001, 2003, FATTORINI & CARPANETO 2001). In our case, this is clearly illustrated by the high dominance of *A. rufus*, which represented more than 52% of the total abundance of tenebrionid beetles collected during our sampling. The second most abundant species, *Ps. helvolus*, represented about 24% of the collected individuals. Thus, the two most abundant species, taken together, represented 76% of the total abundance. This pattern is clearly reflected by the fact that the species abundance distribution followed a geometric

series and it is indicative of a community dominated by *r*-selected species. This is in contrast with findings concerning other environments, where most tenebrionids operate under a *k*-mode of selection (DOYEN & TSCHINKEL 1974) but it is consistent with the fact that sand dune tenebrionid species are typically *r*-selected (see FATTORINI 2008 for a review). As opposed to other environments, the beach-dune systems are strongly influenced by harsh climatic factors and food sources are scarce and rather homogeneous, being mostly represented by vegetable detritus. Thus, these environments can be best colonised by a reduced number of sand-specialised and *r*-selected tenebrionid species that can use decaying organic matter.

Insect species abundance distributions are known to follow a geometric series in communities that are mainly composed of small-sized, relatively short-lived, or opportunistic species with fluctuating populations (GILLER 1984). Generally, the geometric series has been widely used to describe communities of early successions (WHITTAKER 1972, BAZZAZ 1975), which are subject to disturbances (GRAY 1981, NUMMELIN 1998, but see NUMMELIN & KAITALA 2004) or that occupy poor habitats (WHITTAKER 1965, KEELEY & FOTHERINGHAM 2003). Beach-dune ecosystems exhibit all these characteristics, because they can be viewed as an early succession subject to strong disturbances (including the anthropogenic ones) and with a very low productivity, being therefore fully qualified to test the validity of the geometric series model.

In reviewing available data on tenebrionid species abundance in coastal areas and biotopes, FATTORINI (2008) found that the geometric series was an adequate model in all cases. The observed value of the slope of the regression line obtained in this study (-0.25) is also consistent with those known from other coastal systems (which are between -0.29 and -0.25; FATTORINI 2008). The value of *k* indicates the sequential, constant proportion of the total number of individuals in the community. It was about 0.43, which means that the most common species should represent about 43% of individuals in the community, the second most common species would represent half of the remaining half (29%), the third, half of the remaining quarter (14%), and so on. This indicated a strong dominance of few species, as expected for a community inhabiting harsh environments.

Previous studies of variation in insect species overall density found that it tends to decrease from the external to the innermost plant association on sand dunes (COLOMBINI *et al.* 1991, FALLACI *et al.*

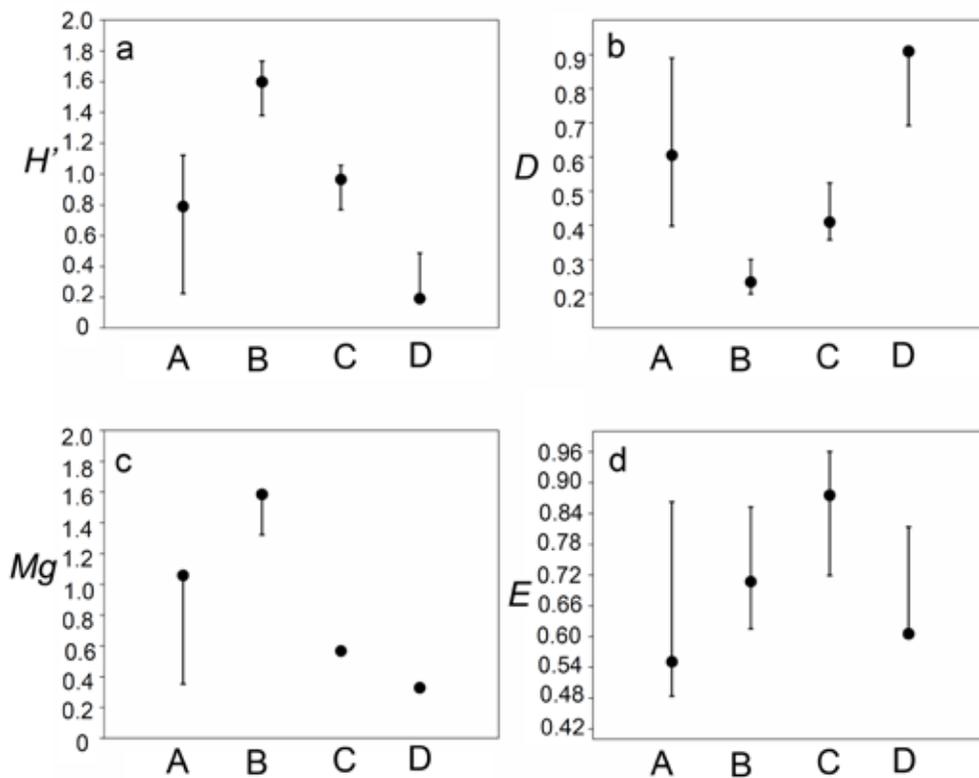


Fig. 4. Values of Shannon diversity (a), Simpson dominance (b), Margalef diversity (c) and Buzas and Gibson evenness (d) for the tenebrionid beetles associated with four biotopes along a beach-dune transect. A: Annual vegetation on drift lines; B: Embryonic shifting dunes; C: Shifting dunes along the shoreline with *Ammophila arenaria*; D: *Malcolmietalia* dune grasslands. Vertical bars represent 95% confidence intervals

1994, CARPANETO & FATTORINI 2001, 2003). Our findings were consistent with this pattern. Tenebrionid density decreased sharply from the first sand accumulations (embryo-dunes) where pioneer plants were very scattered, to the inner fixed dunes, with the highest vegetation cover. The lowest density value was however recorded in the upper beach biotope, the most hostile environment owing to the obvious salt effects and the almost complete lack of vegetation.

According to McLACHLAN (1991), insect species richness should increase proceeding from the beach landwards. This pattern has been also reported for tenebrionids and other coleopterans in Tuscany (COLOMBINI *et al.* 1991, FALLACI *et al.* 1994) along a transect from the beach to the second dune. At within-dune scale, CARPANETO & FATTORINI (2001, 2003), however, did not find variations in species richness, while mean annual values of diversity (measured by Shannon-Wiener index) were similar over the three studied biotopes: *Agropyretum* (EC 2110), *Ammophiletum* (EC 2120) and *Crucianelletum* (EC 2210). In our study with similar biotopes, diversity showed a distinctly hump-shaped pattern analogous with that of density outlined above and contrasting

with that indicated by McLACHLAN (1991). Diversity was low in the upper beach biotope, peaked in the EC 2110 biotope and then decreased proceeding landwards. Thus, the EC 2110 biotope was that with the highest tenebrionid density and diversity and with the lowest dominance. This pattern suggests that the severe halophilous and xerothermic conditions of the seaward margin of the dune, which represent important constraints for most insects, do not act so negatively on the tenebrionid species that live in the EC 2110 biotope.

Although some species were too rare to assess their biotope preference, our data support that at least some of them were distributed with different abundance over the four dune biotopes, thus extending previous findings from other Mediterranean systems (FATTORINI 2008, FATTORINI *et al.* 2012). These differences were likely related to preferences for different characteristics of substratum and detritus. In addition, *Ps. helvolus* seemed to be mostly concentrated on foredunes (embryo dunes and main dune ridge), while its vicariant *Pseudoseriscius normandi* (ESPAÑOL, 1949) appeared to be linked to fixed dunes in the Tyrrhenian coasts (FATTORINI 2008). *Stenosis intermedia* was only found in the embryonic shifting

dunes biotope. However, it is known that this species tends to form aggregations, and all individuals collected in our sampling were found together. Thus, its association with this biotope might be overestimated.

We conducted our sampling in two years in late spring-early summer. Phenological studies have showed that tenebrionids inhabiting sand dunes have their highest activity in this period (FATTORINI 2008). Thus, our snapshot sampling protocol produced a reliable picture of the tenebrionid community during the maximum activity period of the species but did not take into account temporal variations. It would be interesting, in the future, to see if the patterns highlighted in this study vary across seasons.

Conclusions

The present research shows that, when studying the ecology of sand dune organisms, a coastal area can-

not be considered as a single ecological unit, but it is a sequence of different biotopes tightly interconnected and mainly defined by the presence of different plant communities, in turn characterised by differences in insect species diversity. These differences probably mirror different characteristics in the type of substratum and abundance of detritus.

The analysis of a tenebrionid beetle ensemble inhabiting an Adriatic coastal sand dune area showed that different species were distributed with different abundances over the dune biotopes. These results extend previous findings in other Mediterranean areas and indicate that tenebrionid beetles represent an ideal model to analyse coastal sand dune community ecology.

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