

## Biogeography of tenebrionid beetles (Coleoptera: Tenebrionidae) in the circum-Sicilian islands (Italy, Sicily): Multiple biogeographical patterns require multiple explanations

SIMONE FATTORINI

WET – Water Ecology Team, Department of Biotechnology and Biosciences, University of Milano Bicocca, Piazza della Scienza 2, 20126 Milano, Italy; e-mail: simone\_fattorini@virgilio.it

Azorean Biodiversity Group, Departamento de Ciências Agrárias, Universidade dos Açores, Pico da Urze, 9700-042 Angra do Heroísmo, Portugal

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**Abstract.** The tenebrionid beetles on 25 circum-Sicilian islands were studied to determine the influence of island geographical and landscape features on three main intercorrelated biogeographical patterns: (1) species richness, studied using species-area and species environment relationships, (2) species assemblage composition, investigated using Canonical Correspondence Analysis (CCA), and (3) inter-site faunal similarity, investigated using Canonical Correlation Analysis (CANCOR) applied to multidimensional scaling of inter-island faunal dissimilarities. Species richness was mostly influenced by island area and landscape heterogeneity (expressed using various indices of diversity based on land cover categories). When species identities were considered in the CCA, no substantial effect of landscape was detected. Current island isolation did not have a strong influence on species richness, but has a distinct effect in determining species assortments on the remotest islands. Historical influences of Pleistocene landbridge connections were not detectable in species richness relationships using geographical variables in species richness analyses or in assemblage gradients in the CCA, but emerged distinctly from inter-island similarities in the CANCOR.

### INTRODUCTION

Recently there have been advances in Mediterranean island biogeography in terms of the influence of geographical and ecological (environmental) factors on species richness (Foufopoulos & Ives, 1999; Fattorini, 2002b, 2006b, 2007, 2009b, c; Hausdorf & Hennig, 2005; Dapporto & Dennis, 2008a, b), species composition (Dennis et al., 2008; Dapporto & Dennis, 2009; Fattorini, 2011) and inter-island faunal similarities (Dennis et al., 2000; Fattorini, 2002a, 2006a, 2009a, 2010; Hausdorf & Hennig, 2005; Dapporto & Cini, 2007; Dapporto et al., 2007).

There is a large body of literature on the relationships between species richness and geographical and ecological factors, such as area, isolation, age and environmental diversity in the most disparate kinds of archipelagos (Whittaker et al., 2008). These studies typically use correlation analyses, multiple regressions, structural equations or similar techniques to relate species number to the variables of interest (Fattorini, 2002a, b, 2006a, 2007, 2009a, c; Hausdorf & Hennig, 2005; Dapporto et al., 2007; Dapporto & Cini, 2007; Dapporto & Dennis, 2008a).

The importance of geographical and ecological factors in explaining inter-island faunal similarities has received less attention. Studies in this field typically correlate (using Mantel tests) matrices of biogeographical distances with matrices of geographical/environmental distances (see, for example, Hausdorf & Hennig, 2005; Dapporto & Cini, 2007; Fattorini, 2009a, c, 2010) or use a Canonical Correlation Analysis (CANCOR) of a number of dimen-

sions summarizing the biogeographical positions of islands in multidimensional space (e.g. dimensions from Multidimensional Scaling) and values of geographical/environmental variables (see Fattorini, 2006a).

Finally, there are few studies on how geographical and environmental factors may explain species composition on islands and the use of Canonical Correspondence Analysis (CCA) to correlate species distributions with island characteristics was only recently proposed (Fattorini, 2011). No study, however, has integrated these different approaches by simultaneously investigating these three aspects of variation on community structure.

In this paper, these three aspects of the fauna of tenebrionid beetles (Coleoptera: Tenebrionidae) on the islands surrounding Sicily, the largest Mediterranean island, were investigated simultaneously. Sicily is surrounded by a number of small islands, collectively known as the “circum-Sicilian” islands. Some of them form small archipelagos, while others are isolated, and their distance from Sicily varies considerably. The biogeography of the circum-Sicilian islands is particularly complex (e.g. Corti, 1973; Capula, 1994; Corti et al., 1998; Harris et al., 2009), because the islands vary greatly in terms of their geological origin (volcanic vs. sedimentary), paleogeography (some were connected to Sicily or Africa during Pleistocene glaciations, others remained isolated), distance to the main source of colonization (Sicily or Africa), area (Malta, the largest island, has an area of 245.7 km<sup>2</sup>, but most of the islands are smaller than 30 km<sup>2</sup>) and environmental conditions. Moreover, their loca-

tion at the boundary between Europe and Africa makes their faunal composition a mosaic of European and African elements (Fattorini, 2010, 2011) with important conservation implications (Fattorini, 2008b).

Thanks to their low dispersal ability, tenebrionids are excellent biogeographical markers of historical processes (Fattorini, 2001b, 2008a, 2009a, c). They have been repeatedly used to investigate the biogeography of Mediterranean islands (e.g. Fattorini 2002a, 2006a, b, 2009a, c, 2010, 2011; Hausdorf & Hennig, 2005). The distribution of tenebrionid beetles on the circum-Sicilian islands is well known, yet there is no comprehensive biogeographical study. In this paper, the tenebrionid beetles on the circum-Sicilian islands are used to explore how the same geographical and environmental factors influence species richness, species composition of communities and variation in the similarity of communities.

## MATERIAL AND METHODS

### Study islands

The circum-Sicilian islands (Fig. 1) can be grouped into four main archipelagos: the Aeolian Islands (volcanic), the Egadi Islands (sedimentary), the Pelagie Islands (both volcanic and sedimentary) and the Maltese Islands (sedimentary); the remaining two islands, Ustica and Pantelleria (both volcanic), are rather isolated. The Aeolian Islands are separated from Sicily by a sea channel of about 1000–2000 m depth and thus they have always remained apart from Sicily, even during Pleistocene falls in sea level. The sea between the islands (except between Vulcano and Lipari) is also very deep (about 400–1400 m) and prevented Pleistocene inter-island connections. All the Egadi islands are calcareous and at least two islands, Favignana and Levanzo, were repeatedly connected to Sicily either in the Lower and Middle Pleistocene (Calabrian and Ionian stages) between 1.8 million and 126,000 years ago or in the Upper Pleistocene (Tarantian stage) during the Würm glaciation about 18,000 years ago. The island of Ustica is separated from Sicily by a deep and wide sea channel and has always remained apart from Sicily, even during Pleistocene falls in sea level. Lampedusa and Lampione are an emerged portion of the African continental shelf, and were connected to North Africa during the Würm glaciation. Pantelleria and Linosa were not connected to mainland areas (Sicily or North Africa). Finally, the Maltese Islands were connected to Sicily and probably to North Africa during the Pleistocene, but their separation from Africa occurred long before that from Sicily. For detailed information on these islands see Corti (1973), Mazzola et al. (2001) and The Maltese Islands Multimedia Encyclopedia (2011).

### Measurements of geographical and environmental variables

The geographical parameters are summarized in Table 1. Both island area and isolation are important factors regulating species occurrences on islands (Whittaker, 1998). As measures of island isolation, I considered here both island distance to Sicily or North Africa (both considered as the closest “mainland” areas) and to the nearest island (Table 1); see Fattorini (2010) for details.

Sea level changed greatly during the Pleistocene, determining both inter-island and island-mainland connections. As a rule, falls in sea level connected areas above a depth of 200–150 m. It can be assumed that, during Pleistocene falls in sea level, lower depths permitted longer connections with wider land bridges between islands and/or to the mainland. Thus, to study the influence of paleogeography on species richness and composition, I

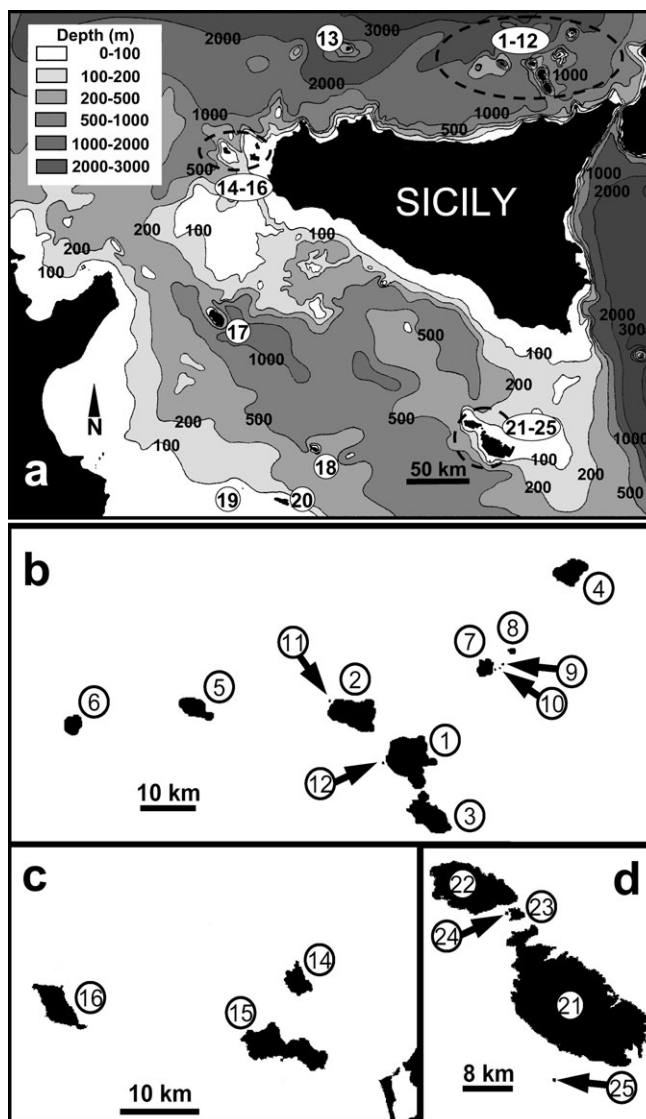


Fig. 1. Map of the study area with sea depths (a). Island positions within archipelagos are detailed for the Aeolian (b), Egadi (c) and Maltese Islands (d). Islands names are as follows: 1 – Lipari, 2 – Salina, 3 – Vulcano, 4 – Stromboli, 5 – Filicudi, 6 – Alicudi, 7 – Panarea, 8 – Basiluzzo, 9 – Lisca Bianca, 10 – Bottaro, 11 – Scoglio Faraglione, 12 – Pietra del Bagno, 13 – Ustica, 14 – Levanzo, 15 – Favignana, 16 – Marettimo, 17 – Pantelleria, 18 – Linosa, 19 – Lampione, 20 – Lampedusa, 21 – Malta, 22 – Gozo, 23 – Comino, 24 – Cominotto, 25 – Filfla.

used sea depths among islands and between islands and the mainland (Crowell, 1986).

To characterize environmental conditions, I calculated the extent of island surface occupied by different land cover categories according to the European Corine Land Cover classification. Although somewhat crude, Corine land cover categories are extensively used to express species-environment relationships (e.g., Lobo & Martín-Piera, 2002; Stefanescu et al., 2004; Maes et al., 2005). A total of 24 land cover categories were found on the circum-Sicilian islands. This is too many predictors compared to the small number of islands composing the archipelago. Moreover, some categories were represented by very small patches or can be easily combined into broader categories. Thus, I constructed the following main categories of landscape types (Table 2): Built up areas (including Continuous

TABLE 1. Geographical variables for the circum-Sicilian islands. *S* – number of species; *A* – Area (km<sup>2</sup>); *Ds* – Distance to Sicily (km); *Da* – Distance to North Africa (km); *Di* – Distance to the nearest island (km); *SDs* – Sea depth to Sicily (m below sea level); *SDa* – Sea depth to Africa (m below sea level); *SDi* – Sea depth to the nearest island (m below sea level). *X*<sub>1</sub>, *X*<sub>2</sub> and *X*<sub>3</sub> are the three dimensions extracted by Non-metric Multidimensional Scaling from a matrix of inter-island faunal dissimilarity (Kulczynski 2 index).

Island	<i>S</i>	<i>A</i>	<i>Ds</i>	<i>Da</i>	<i>Di</i>	<i>SDs</i>	<i>SDa</i>	<i>SDi</i>	<i>X</i> <sub>1</sub>	<i>X</i> <sub>2</sub>	<i>X</i> <sub>3</sub>
1. Lipari	32	37.29	28	370	1	780	1500	10	-0.306	-0.049	0.075
2. Salina	24	26.38	39	365	4	780	1500	366	-0.392	0.169	-0.178
3. Vulcano	22	20.87	21	375	1	780	1500	10	-0.181	0.248	0.073
4. Stromboli	25	12.19	58	405	18	1200	1500	1281	-0.255	0.326	-0.330
5. Filicudi	15	9.49	46	345	15	1500	1500	1281	-0.629	-0.038	0.416
6. Alicudi	18	5.1	53	330	15	1500	1500	1281	-0.562	0.040	0.220
7. Panarea	22	3.34	42	390	14	780	1500	600	-0.582	-0.033	-0.010
8. Basiluzzo	3	0.29	43.5	394	3.5	780	1500	80	-1.004	0.603	0.339
9. Lisca Bianca	4	0.0413	42	390	3	780	1500	50	-0.917	0.290	-0.152
10. Bottaro	7	0.0073	42	390	2.75	780	1500	50	-0.831	-0.032	-0.102
11. Scoglio Faraglione	4	0.0049	39	365	0.27	780	1500	10	-0.737	-0.036	-0.628
12. Pietra del Bagno	3	0.0021	28	370	0.45	780	1500	20	-0.283	-0.089	-0.596
13. Ustica	26	8.6	53	255	100	1500	1500	1500	-0.334	-0.416	0.326
14. Levanzo	18	5.61	12	152	4	42	400	42	-0.108	-0.468	0.484
15. Favignana	28	19.7	8	140	4	42	400	42	0.001	-0.410	0.326
16. Marettimo	16	12.06	35	130	15	145	400	145	0.314	-0.322	1.046
17. Pantelleria	23	86	95	67	115	500	500	500	0.292	-1.255	0.066
18. Linosa	19	5.34	162	163	40	500	400	400	0.247	-1.021	-0.675
19. Lampione	4	0.025	220	130	18	500	100	100	0.234	1.762	-0.285
20. Lampedusa	28	20.2	195	120	18	500	100	400	0.646	-0.527	-0.879
21. Malta	43	246	93	292	6	200	500	100	0.871	0.018	0.144
22. Gozo	26	67	82	285	6	200	500	100	1.121	0.015	0.033
23. Comino	10	3.5	85	295	2	200	500	100	0.961	0.417	-0.441
24. Cominotto	2	0.25	85	295	0.1	200	500	100	1.389	0.378	-0.413
25. Filfla	3	0.06	100	292	5	200	500	100	1.047	0.432	1.141

urban fabric, Discontinuous urban fabric, Industrial or commercial units, Port areas, Airports, Mineral extraction sites, Dump Sites, Green urban areas, and Sports and Leisure facilities), Cultivation (including Vineyards, Non-irrigated arable land, Natural grassland, Annual crops associated with permanent crops, Complex cultivation patterns, and Land principally occupied by agriculture, with significant areas of natural vegetation), Coniferous forest, Broad-leaved and Mixed forests, Sclerophyllous vegetation, Bare rock and Sparsely vegetated areas, and Wet areas (including Salt marshes, Salines, and Water bodies). Even if these broad landscape units are coarse in comparison to the scale at which insects perceive small-scale environmental heterogeneity, they correspond well to distinct keystone structures (Tews et al., 2004) for tenebrionid species. In particular, each of the seven classes used here corresponded to different microclimate conditions, food resources, and soil characteristics, which are among the most important factors shaping tenebrionid communities in the Mediterranean (Fattorini, 2008b).

Geographical distances and land cover categories were obtained from the GIS of the Italian Ministry of the Environment and Protection of the Territory and Sea (2009) and from Malta Environment and Planning Authority (2009). Sea depths were obtained from bathymetric maps mainly from the Istituto Idrografico della Marina (1997).

#### Biological data

Presence/absence data of individual species on each island (Appendix 1) are based on extensive field surveys made by specialists with similar sampling efforts among islands; the faunal inventories are fairly complete. A total of 107 native taxa are known from these islands.

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 circum-Sicilian islands, is arguably arbitrary and the exclusion of subspecies could result in a significant underestimate of endemic island tenebrionid diversity. Thus, I considered both species and subspecies as “evolutionarily significant units” (Ryder, 1986) and included both categories in all analyses. The validity of the endemic subspecies *Heliopathes avarus donatellae* (Canzoneri, 1970) is disputed and the identity of the endemic species *Opatrum melitense* Küster, 1849 is uncertain. Both taxa have been provisionally considered as valid. On the basis of the original description, the differentiation of *Heliopathes avarus dwejrensis* Scupola & Mifsud, 2001 from Gozo seems very subtle. The same is the case for *Probatiscus cossyrensis* Sparacio, 2007, which was recently separated from *Probatiscus anthrax* Seidlitz, 1896. All analyses were performed including and excluding these two taxa. Only results with all taxa included are presented, because exclusion of these two taxa produced virtually identical results.

Finally, cosmopolitan species strictly associated with human food, such as *Palorus subdepressus* (Wollaston, 1864), *Gnato-cerus cornutus* (Fabricius, 1798), *Alphitobius diaperinus* (Panzer, 1796), *Tenebrio* spp. and *Tribolium* spp. were excluded from all analyses to reduce the risk of confounding natural patterns with effects of man. A list of 45 references used to compile presence/absence data is given in Appendix 1.

TABLE 2. Extent (km<sup>2</sup>) of land cover categories and values of environmental (landscape) heterogeneity indices. *N* – number of land cover categories present on an island. Land cover categories: *BU* – Built up areas; *CU* – Cultivation; *CO* – Coniferous forests; *BL* – Broad-leaved and Mixed Forests; *SC* – Sclerophyllous vegetation; *BR* – Bare rock and sparsely vegetated areas; *WA* – Wet areas. Landscape heterogeneity indices: *C* – Simpson dominance index; *H* – Shannon index;  $e^{H/N}$  – Buzas and Gibson evenness; *J* – Pielou equitability;  $D_{Mg}$  – Margalef richness index; *d* – Berger-Parker dominance.

Islands	<i>N</i>	Landcover categories							Heterogeneity indices					
		<i>BU</i>	<i>CU</i>	<i>CO</i>	<i>BL</i>	<i>SC</i>	<i>BR</i>	<i>WA</i>	<i>C</i>	<i>H</i>	$e^{H/N}$	<i>J</i>	$D_{Mg}$	<i>d</i>
1. Lipari	4	9.397	13.196	0.000	0.000	8.198	6.498	0.000	0.268	1.352	0.967	0.976	0.285	0.354
2. Salina	3	3.897	3.298	0.000	0.000	19.185	0.000	0.000	0.566	0.774	0.723	0.705	0.197	0.727
3. Vulcano	5	3.598	6.785	0.000	0.514	7.505	2.467	0.000	0.279	1.380	0.795	0.857	0.402	0.360
4. Stromboli	3	1.125	0.000	0.000	0.000	7.033	4.032	0.000	0.451	0.903	0.823	0.822	0.213	0.577
5. Filicudi	3	0.000	1.998	0.000	0.000	6.693	0.799	0.000	0.549	0.783	0.729	0.712	0.218	0.705
6. Alicudi	3	0.400	0.000	0.000	0.000	3.000	1.700	0.000	0.463	0.878	0.802	0.799	0.234	0.588
7. Panarea	3	0.786	0.000	0.000	0.000	1.866	0.688	0.000	0.411	0.991	0.898	0.902	0.247	0.559
8. Basiluzzo	1	0.000	0.000	0.000	0.000	0.290	0.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000
9. Lisca Bianca	1	0.000	0.000	0.000	0.000	0.000	0.000	0.041	1.015	-0.007	0.993	0.000	0.000	1.000
10. Bottaro	1	0.000	0.000	0.000	0.000	0.000	0.000	0.007	1.088	-0.044	0.957	0.000	0.000	1.000
11. Scoglio Faraglione	1	0.000	0.000	0.000	0.000	0.005	0.000	0.000	1.501	-0.249	0.780	0.000	0.000	1.000
12. Pietra del Bagno	1	0.000	0.000	0.000	0.000	0.000	0.000	0.002	1.103	-0.051	0.950	0.000	0.000	1.000
13. Ustica	5	1.163	2.609	1.013	0.000	3.133	0.681	0.000	0.263	1.453	0.855	0.903	0.442	0.364
14. Levanzo	2	0.000	1.006	0.000	0.000	4.604	0.000	0.000	0.706	0.470	0.800	0.678	0.116	0.821
15. Favignana	3	0.861	13.864	0.000	0.000	4.975	0.000	0.000	0.561	0.732	0.693	0.666	0.202	0.704
16. Marettimo	3	0.000	0.728	0.000	0.000	10.226	1.107	0.000	0.731	0.528	0.565	0.481	0.213	0.848
17. Pantelleria	5	8.671	51.041	6.196	0.000	19.801	0.000	0.291	0.421	1.088	0.594	0.676	0.352	0.594
18. Linosa	3	0.854	3.117	0.000	0.000	1.369	0.000	0.000	0.432	0.956	0.867	0.871	0.233	0.584
19. Lampione	1	0.000	0.000	0.000	0.000	0.000	0.000	0.025	1.000	0.000	1.000	0.000	0.000	1.000
20. Lampedusa	4	2.898	5.741	0.857	0.000	10.704	0.000	0.000	0.384	1.107	0.756	0.798	0.303	0.530
21. Malta	7	80.380	126.750	0.694	1.488	33.156	3.272	0.261	0.391	1.089	0.425	0.560	0.483	0.515
22. Gozo	4	29.458	27.761	0.000	0.000	9.562	0.219	0.000	0.385	1.023	0.695	0.738	0.270	0.440
23. Comino	1	0.000	0.000	0.000	0.000	3.500	0.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000
24. Cominotto	1	0.000	0.000	0.000	0.000	0.250	0.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000
25. Filfla	1	0.000	0.000	0.000	0.000	0.060	0.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000

### Data analysis

Correlation of species richness with geographical and environmental variables

One of the most controversial issues in island biogeography is the importance of “habitat diversity” and area per se in determining species numbers (Whittaker, 1998; Fattorini, 2006a; Hortal et al., 2009). To express “habitat diversity”, several authors have used the number of biotopes occurring in study areas (see Fattorini, 2006a; Tognelli & Kelt, 2004; Hortal et al., 2009). In addition to the number (*N*) of land cover categories defined above, I used selected synthetic indices of environmental (landscape) heterogeneity. Although Shannon’s index is typically used (e.g. Lobo & Martín-Piera, 2002; Nogués-Bravo & Martínez-Rica, 2004; Stefanescu et al., 2004; Maes, 2005), studies on community ecology have demonstrated that no single diversity index encompasses all the characteristics of an ideal index (Magurran, 1988; Krebs, 1999). Therefore, I also used the following indices derived from those used in studies on community ecology (Legendre & Legendre, 1998; Magurran, 1988, 2004; Hayek & Buzas, 2010) to express richness, dominance, evenness and relative abundance:

– Simpson dominance index:  $C = \sum \left(\frac{A_i}{A}\right)^2$ , where  $A_i$  is the extent of the land cover category *i*, and *A* is the total surface of the island. *C* can vary from 0 if all land cover categories have equal extent to 1 if one category dominates the landscape completely.

– Shannon index (entropy):  $H = -\sum \frac{A_i}{A} \ln\left(\frac{A_i}{A}\right)$ . *H* ranges from 0, if one land cover category dominates the landscape completely, to arbitrarily high values for landscapes with many categories, each with a small extent.

– Buzas and Gibson evenness:  $e^{H/N}$ , where *N* is the number of categories and *H* is the Shannon index.

– Pielou equitability (evenness):  $J = H/\ln N$ .

– Margalef richness index:  $D_{Mg} = (N-1)/\ln(A)$ .

– Berger-Parker dominance:  $d = A_{max}/A$ , where  $A_{max}$  is the extent of the dominant land cover category.

Species richness can be related to environmental variables, such as measures of island area, distances and environmental heterogeneity in different ways. The relationship between number of species and area (species-area relationship, SAR) was here best modelled with the power function  $S = CA^z$ , where *S* is the number of species, *A* is an island’s area, and *C* and *z* are fitted parameters (Martín & Goldenfeld, 2006; Fattorini, 2006b; Dengler, 2009).

The power function may be fitted as  $\ln S = \ln C + z \ln A$  using ordinary linear regression, or directly as  $S = CA^z$  with a non-linear regression. Although the link function is identical, the two models have different distributional assumptions and are not statistically equivalent for least-square regression (see Williams et al., 2009 for details). Because there is no biological or statistical preference for either model (Dengler, 2009), both were used in this study. The untransformed model was applied using a Quasi-Newton algorithm with Statistica 6.0 software. As suggested by

Williams et al. (2009), residuals were examined with Shapiro-Wilk statistics to determine which distributional assumption was the most appropriate for modelling the dataset. These tests indicated a marginally significant lack-of-fit for the log-transformed model ( $W = 0.916$ ,  $P = 0.04$ ), but not for the power function fitted using non-linear regression ( $W = 0.970$ ,  $P = 0.65$ ). Thus, preference was given to the untransformed model.

The resulting  $z$ -value ( $z \approx 0.25$ ) matched values typically found for island systems (Rosenzweig, 1995; Drakare et al., 2006). The SAR is a consistent phenomenon in insular ecosystems, and the best way to consider other sources of variation in species numbers is through the analysis of residuals from species-area regressions (Crowell, 1986; Rosenzweig, 1995; Price, 2004). Thus, residuals from the SAR were correlated with other geographical variables and environmental heterogeneity indices using Spearman correlation tests, which simply assume monotonic relationships without any reference to particular functions.

#### Analysis of variation in species composition

Variation in species composition between the islands was analysed with CCA using the CANOCO program, version 4.5A (Ter Braak & Šmilauer, 2002). A Detrended Correspondence Analysis with the option “detrending-by-segments” (Hill & Gauch, 1980) produced a first axis of 9.239 SD, which is more than 2 SD units and hence indicates that CCA is suitable for this data set (Ter Braak & Prentice, 1988).

Significance of individual environmental parameters (geographical and environmental variables) was tested using a forward selection with 999 Monte Carlo permutations (see Fattorini, 2011 for details). The influence of geographical and landscape variables were tested separately. Both the extent of different landscape categories and their proportions can be important characteristics of the landscape of a given island. Thus, separate CCAs were performed using alternatively the raw and proportional extent of landscape categories.

#### Inter-island biogeographical similarity

Canonical Correlation Analysis (CANCOR) was used to analyse the influence of geographical and landscape variables on inter-island biogeographical similarity. The original presence/absence matrix was then subject to a non-metric multidimensional scaling (NMDS) using the Kulczynski 2 coefficient to construct a dissimilarity matrix (for a discussion of the use of this coefficient in biogeographical analyses, see Hausdorf & Hennig, 2005). This technique is designed to construct a “map” showing the relationships between a number of objects, given only a table of distances or similarity between them, and is often best at capturing patterns in community data when similarity coefficients are used (Legendre & Legendre, 1998). The goodness of results obtained by NMDS was measured as stress values. On the basis of the increase in stress values when the number of dimensions was decreased (Shi, 1993) the retention of three dimensions was considered to be sufficiently representative. These three dimensions were used as dependent variables in CANCORs. Separate CANCORs were performed for geographical and environmental variables to meet “rule C” of McGarigal et al. (2000). Inter-island faunal similarity was also investigated by cluster analysis using the Kulczynski 2 coefficient as a measure of distance and the UPGMA (Unweighted pair-group method, arithmetic average) amalgamation rule. NMDS and CANCORs were performed using Statistica 6.0 software.

Both CCA and CANCOR investigate the effects of geographical/environmental variables on species composition from complementary points of view and cannot be considered

alternative approaches (McGarigal et al., 2000). CCA identifies geographical/environmental gradients which mainly influence species composition of sites, whereas CANCOR correlates dominant gradients in species assemblages with geographical/environmental gradients. Thus, CCA is particularly useful for investigating the influence of geographical/environmental gradients on beta diversity (second level of abstraction sensu Tuomisto & Ruokolainen, 2006) whereas CANCOR investigates the importance of geographical/environmental gradients in regulating variation in beta diversity, i.e. “variation in variation in community composition data” — third level of abstraction sensu Tuomisto & Ruokolainen (2006).

## RESULTS

### Species richness

Area was an important correlate of species richness and the species-area relationship (SAR) was well modelled by a power function ( $S = 11.5 A^{0.23}$ ;  $R^2 = 0.84$ ). When residuals of the SAR were plotted against other geographical variables, no relationship was found (Table 3). Species richness was also tightly correlated with all measures of landscape heterogeneity (Table 3). When residuals of the SAR were correlated with landscape heterogeneity indices, significant correlations were found for Pielou equitability and, possibly, for Simpson dominance and Berger-Parker dominance (Table 3). These results suggest that relationships between species richness and landscape heterogeneity were mainly through area. When the stronger effect of area was removed, the influence of landscape heterogeneity was less evident, although there is an indication that richness tends to increase with landscape diversity and equitability and decrease with landscape homogeneity (Table 3).

TABLE 3. Values of Spearman correlation coefficients of species richness and residuals from the species-area relationship (SAR) with geographical and landscape parameters. Abbreviations are the same as those in Tables 1 and 2. Residuals from SAR were calculated using the power function. Values in bold are significant at  $P < 0.05$ .

	Correlation coefficients between number of species and environmental parameters	Correlation coefficients between residuals from SAR and environmental parameters
<i>A</i>	<b>0.851</b>	0.082
<i>D<sub>s</sub></i>	-0.040	-0.194
<i>D<sub>a</sub></i>	-0.250	0.101
<i>D<sub>i</sub></i>	<b>0.409</b>	0.188
<i>SD<sub>s</sub></i>	-0.024	0.281
<i>SD<sub>a</sub></i>	-0.114	0.133
<i>SD<sub>i</sub></i>	0.232	0.081
<i>N</i>	<b>0.873</b>	0.314
<i>C</i>	<b>-0.840</b>	<b>-0.403</b>
<i>H</i>	<b>0.831</b>	0.364
<i>e<sup>H</sup>/N</i>	<b>-0.628</b>	-0.090
<i>J</i>	<b>0.737</b>	<b>0.569</b>
<i>D<sub>Mg</sub></i>	<b>0.828</b>	0.358
<i>d</i>	<b>-0.874</b>	<b>-0.504</b>

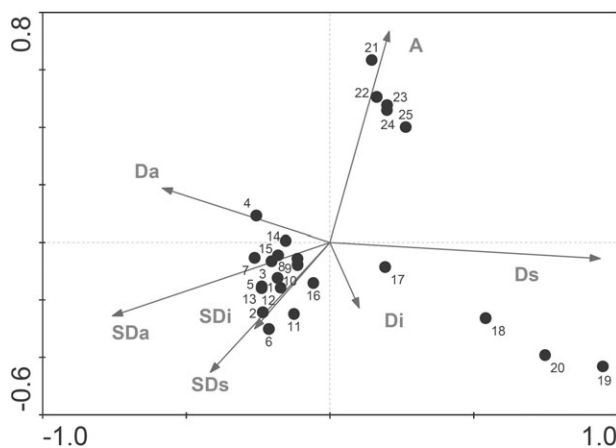


Fig. 2. The results of the CCA of the effect of island characteristics in determining the species composition of tenebrionid beetles on circum-Sicilian islands. The relative importance of individual geographical variables is expressed by the length of the respective vectors. A – Area; Ds – Distance to Sicily; Da – Distance to North Africa; Di – Distance to the nearest island; SDs – Sea depth to Sicily; SDa – Sea depth to Africa; SDi – Sea depth to the nearest island.

### Variation in species composition

The constrained ordination (CCA) biplot for geographical variables (Fig. 2) resulted in relatively high eigenvalues and cumulative percentage variances, indicative of a well structured data set (Table 4). Moreover, there were strong species-geography correlations with all four axes, which together accounted for about 90% of the variance explained by the geographical data. Table 4 also shows the correlation coefficients of the geographical variables with four axes of the ordination, the results of the automatic forward selection of the geographical variables, additional fit given by each step and their statistical significance. Distance to Sicily was very strongly related to axis 1, whereas island area was associated with axis 2. Axis 1 was also negatively related to maximum water depth between the island in question and Africa (referred to as “depth to Africa”). Distance to Africa and the nearest island were related to axis 3; the respective rela-

tionships were negative and positive. No variable was distinctly associated with axis 4. Of these variables, distance to Sicily and distance to Africa have significant conditional effects, whilst water depth to Africa was marginally non-significant. Area and distance to Africa showed similar increases in eigenvalue, whereas distance to Sicily had a substantially higher value of additional fit. Island distance to Sicily was particularly important in determining species composition on Pantelleria and the Pelagie Islands. By contrast, area was particularly important for the Maltese Islands.

Using raw values of land cover categories, the constrained ordination biplot resulted in low eigenvalues and cumulative percentage variances, indicative of a “noisy” data set (Table 5). However, there were strong species-environment correlations with all three axes, which together accounted for 84% of the variance explained by the environmental data. Use of percentage values of land cover produced even worse results (Table 5). No variable had a significant effect when raw values were used, whilst the percentage of cultivated and grassland areas was the only variable that had a (marginally) significant value ( $F$ -ratio = 1.55,  $P$  = 0.05) when percentage data were used.

### Inter-island biogeographical similarity

Cluster analysis based on Kulczynski 2 inter-island faunal similarity and UPGMA clustering method produced a dendrogram that reflects the geographical groupings of the islands (Fig. 3). The first basic split separates the Maltese Islands from all other islands. The latter are subdivided into two main clusters: in one are the islands of the Sicilian Channel (Pantelleria and Pelagie) and in the other larger one are the islands closer to Sicily. In this large cluster, two smaller clusters can be identified: one grouping the Egadi Islands with Ustica and another including the Aeolian Islands and islets. Although three dimensions were retained from NMDS and introduced in CANCEORS, a biplot of the first two dimensions indicates that these are sufficient to reflect inter-island relationships (Fig. 4). The third dimension was also not significant in CANCEORS (see below).

TABLE 4. Results ( $F$ -statistics) of CCA for the geographical variables.  $\lambda_a$  indicates the increase in eigenvalue (additional fit).  $P$  indicates the significance level of the conditional effects based on Monte Carlo tests (999 random permutations). Variables are the same as in Table 1.

Variable	$\lambda_a$	$P$	$F$	Weighted correlations			
				Axis 1	Axis 2	Axis 3	Axis 4
<i>Ds</i>	0.51	0.004	2.682	0.901	-0.051	-0.142	-0.177
<i>A</i>	0.35	0.083	1.900	0.211	0.687	0.221	-0.336
<i>Da</i>	0.34	0.016	1.930	-0.594	0.208	-0.614	-0.355
<i>SDa</i>	0.29	0.060	1.720	-0.744	-0.224	-0.297	-0.420
<i>Di</i>	0.25	0.134	1.516	0.139	-0.224	0.682	-0.327
<i>SDi</i>	0.16	0.480	0.987	-0.255	-0.281	0.000	-0.231
<i>SDs</i>	0.14	0.576	0.845	-0.414	-0.415	-0.228	-0.447
Eigenvalues				0.555	0.456	0.376	0.207
Cumulative % variance				11.3	20.6	28.3	32.6
Cumulative species-geography relationship				27.1	49.3	67.7	77.8
Species-geography relationship				0.964	0.961	0.963	0.899

TABLE 5. Eigenvalues, cumulative explained variance (%), cumulative species-environment relationship (%) and species-environment correlations for the first four constrained ordination axes of CCA.

	Axis 1	Axis 2	Axis 3	Axis 4
Land cover (raw values)				
Eigenvalues	0.421	0.382	0.260	0.195
Cumulative % variance	8.6	16.4	21.7	25.7
Cumulative species-environment relationship	25.9	49.3	65.3	77.3
Species-environment relationship	0.952	0.956	0.862	0.842
Land cover (% values)				
Eigenvalues	0.378	0.304	0.256	0.159
Cumulative % variance	7.7	13.9	19.1	22.4
Cumulative species-environment relationship	28.1.4	50.7	69.7	81.5
Species-environment relationship	0.870	0.304	0.256	0.159

### CANCOR with geographical variables

With all canonical roots together, that is, without any root removed, the overall CANCOR analysis gave  $\chi^2_{(21)} = 61.30$ ,  $P = 0.000008$  (canonical  $R^2 = 0.87$ ). For the second root,  $\chi^2_{(12)} = 24.27$ ,  $P = 0.02$  (canonical  $R^2 = 0.67$ ). Finally, the third root was clearly not significant (canonical  $R^2 = 0.18$ ,  $\chi^2_{(5)} = 3.73$ ,  $P = 0.82$ ).

Total percentage of variance extracted in the X set (53.6%) was mainly represented by the variance extracted by the first and second roots, while redundancy highlighted the importance of the first root (Table 6). Total redundancy for the Y set was 57.3%. Looking at the factor structure (structure coefficients or canonical loadings), the first dimension extracted by NMDS was mainly

TABLE 6. Results from CANCOR with all canonical roots analysed. Variables are the same as in Table 1.

	Factor Structure		
	Root 1	Root 2	Root 3
Distributional patterns (coordinates from Non-metric Multidimensional Scaling)			
Dimension 1	-0.993	-0.044	-0.111
Dimension 2	-0.098	-0.811	0.577
Dimension 3	-0.066	0.584	0.809
Variance extracted	0.333	0.333	0.333
Redundancy	0.288	0.224	0.061
Geographic characteristics			
<i>A</i>	0.010	0.176	-0.202
<i>Ds</i>	0.501	-0.776	-1.953
<i>Da</i>	-1.748	-0.695	1.888
<i>Di</i>	-0.531	0.302	0.062
<i>SDs</i>	-0.733	-0.570	2.996
<i>SDa</i>	3.061	0.302	-4.565
<i>SDi</i>	0.212	0.470	-0.985
Variance extracted	0.269	0.121	0.146
Redundancy	0.233	0.081	0.027
Eigenvalues	0.865	0.671	0.183

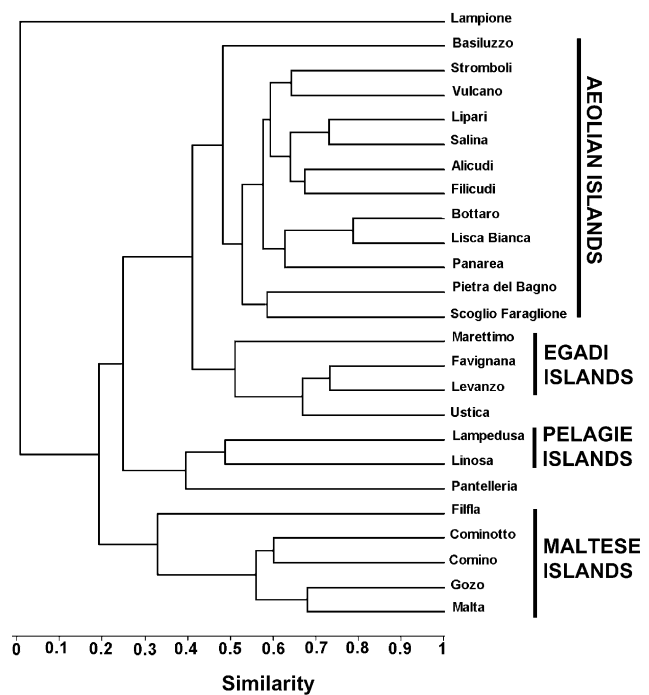


Fig. 3. The relationships between circum-Sicilian islands based on tenebrionid beetles using the Kulczynski 2 index and UPGMA clustering.

influenced by distance to North Africa and sea depth to Africa, while the second one was influenced by distance to Sicily. The third dimension of NMDS was represented by the non-significant root 3. Thus, current and past isolation from Africa appear to be mainly responsible for the biogeographic relationships among islands represented by the first axis of the NMDS. Current isolation from Sicily is responsible for the biogeographic relationships among islands represented by the second axis of the NMDS (Fig. 4).

### CANCOR with environmental variables

With all canonical roots together, CANCOR analysis using raw data of land cover gave  $\chi^2_{(21)} = 19.80$ ,  $P = 0.53$

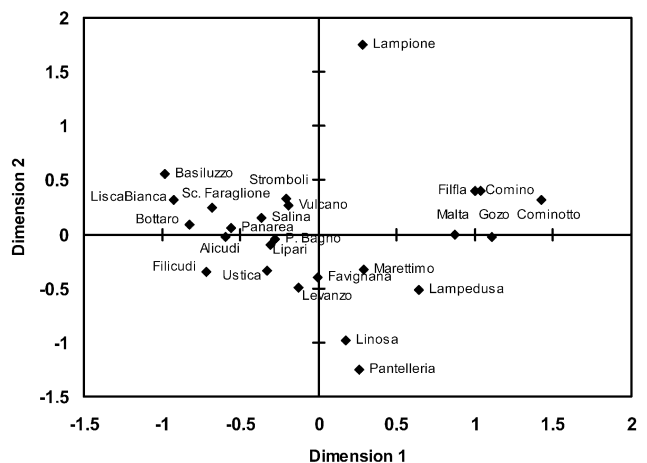


Fig. 4. The relationships between circum-Sicilian islands based on tenebrionid beetles using the Kulczynski 2 index and Non-metric Multidimensional Scaling.

(canonical  $R^2 = 0.56$ ) and percentage of land cover gave  $\chi^2_{(21)} = 20.85$ ,  $P = 0.47$  (canonical  $R^2 = 0.52$ ). Thus, in both cases, there was no significant correlation between biogeographical patterns and land cover.

## DISCUSSION

The species-area relationship is the most widespread and best documented pattern in macroecology (cf. Rosenzweig, 1995). For the tenebrionids of the circum-Sicilian islands, island area accounted for most of the variability in species numbers, as previously observed for other Mediterranean islands (e.g. Fattorini, 2002a, 2009a, 2009b, c). Their species richness increased with various measures of environmental diversity and decreased with environmental homogeneity. This accords with the fact that landscape diversity typically increases the diversity of generalist insects (Jonsen & Fahrig, 1997; Krauss et al., 2003).

Relationship between species richness and environmental diversity in island biogeography is typically investigated within the wider framework of the species-habitat diversity hypothesis (see Hortal et al., 2009). However, this may be incorrect as the term “habitat” is often misused. For example, previous studies using “number of habitats” used, in reality, number of biotopes; see Dennis (2010) for a distinction between habitat and biotope. A recent model by Kadmon & Allouche (2007) found species richness to follow a uni-modal distribution in relation to increasing biotope numbers (“habitat diversity” according to their use): species diversity initially increases with number of biotopes from a very simple island towards biotope-wise more complex islands, until a maximum species richness is reached, and then it declines because too many biotope types imply that the total areas of individual biotope types are small, reducing the area of suitable biotopes for any given species. In contrast, Hortal et al. (2009) found that species richness on islands usually increases with the number of biotopes and never decreases. Results obtained for the tenebrionids on the circum-Sicilian islands support the findings of Hortal et al. (2009) not only for the number of biotopes but also for various measures of environmental diversity.

In the last few decades, there has been a continuous debate on whether area per se or “habitat” diversity is more important in influencing species richness on islands. Some studies support the idea that the species-area relationship derives from the fact that larger islands have a greater “habitat diversity” (Báldi, 2008; Jonsson et al., 2009), others indicate that there is a strong effect of area per se (Nilsson et al., 1988; Marini et al., 2010) and many report a mixed effect (Ricklefs & Lovette, 1999; Kallimanis et al., 2008). For the tenebrionids of the circum-Sicilian islands, correlations between residuals from the species-area relationship and measures of landscape heterogeneity suggest that some of the variation in species richness not explained by area can be attributed to landscape heterogeneity. Thus, both area and landscape diversity may contribute to species richness.

Distances to the nearest island and to the mainland were not identified as of any statistical importance in affecting species numbers. This suggests that, in general, species richness on the circum-Sicilian islands is not regulated by “stepping stone” processes or “mainland-island” dynamics (for an example within the sub-system of the Aeolian Islands, see Fattorini, 2010). This is probably a consequence of two characteristics of the study system. First, the circum-Sicilian islands are a composite assemblage of islands and “stepping stone” processes or “mainland-island” dynamics may be important for some islands (Fattorini, 2010) but not for others. Second, tenebrionids are, in general, sedentary animals and their occurrence on islands is typically better explained by relict models (i.e., by colonization via land-bridge connections followed by local extinction after disconnection) than equilibrium ones (i.e., by current overseas dispersal) (Fattorini, 2002b, 2006a, 2007). Although geographical distances did not exert a clear influence on species richness, they are important in determining species composition. In particular, distance to Sicily exerted an important influence in determining species composition on Pantelleria and the Pelagie Islands, which are among the remotest islands, whereas the distance to Africa was of less importance. These results suggest that colonization of all islands occurred mainly from Sicily and the process depended on the dispersal ability of each species. Lomolino (2000) stressed the importance of differences in the colonization ability of individual species to explain distributional patterns in island systems. The importance of sources and the observation that the impoverishment of island faunas is influenced by species characteristics was recently demonstrated for butterflies on the Tyrrhenian islands (Dapporto & Dennis, 2008a, 2009). In this respect, species assemblages on highly isolated islands should be strongly affected by isolation, which selects the most “successful” colonizers from the species pool in the source areas.

Island area was particularly important in regulating species assemblages on the Maltese islands. This small archipelago includes the largest islands and is also very isolated. Thus, it is a well defined sub-system and the largest island, Malta, may act as a source of species for its smaller, satellite islands.

The circum-Sicilian islands are biogeographically strongly structured, as revealed by cluster analysis and multidimensional scaling. Both techniques show that faunal similarities among islands reflect their geographical and paleogeographical relationships. CANCORs revealed a strong influence of distance and sea depth to Africa. Thus, although species assemblages on islands are not influenced by relationships with Africa, this is an important factor for inter-island similarity. In particular, position of the Maltese Islands and Lampedusa along the first dimension of multidimensional scaling, related to current and past isolation from Africa, fits with the paleogeographical history of these islands. Relationships of Lampedusa with the African mainland are also testified by the occurrence of African elements, such as



*Allophylax costatipennis costatipennis* (Lucas, 1846), *Pachychila tazmaltensis* Desbrochers des Loges, 1881, *Eutagenia aegyptiaca tunisea* Normand, 1936, *Gonocephalum perplexum* (Lucas, 1846) and *Microtelus lethierryi* Reiche, 1860.

Endemicity levels vary considerably among islands, as a result of their different paleogeographical history. For the Aeolian archipelago, which is very close to Sicily, with a paleogeographical distance strongly reduced during Pleistocene regressions, only one endemic species (*Nalassus pastai* Aliquò, Leo & LoCascio, 2006 from Vulcano) is known. Two endemic taxa are known from the Egadi Islands, both from Marettimo, the only island in the Egadi group that remained disconnected from Sicily during Pleistocene regressions. One endemic taxon is known from Ustica and one from Pantelleria. Isolation of these two islands could have favoured some morphological differentiation in their populations, but because of their recent origin, speciation could not occur or be completed until present. The Pelagie Islands are remote and very ancient islands hosting several endemics (four on Lampedusa, two on Lampione, an islet of just 0.03 km<sup>2</sup> with four tenebrionid taxa, and one – *Machlopsis doderoi* Gridelli, 1930 – endemic to Lampedusa and Lampione). No exclusive endemic is known from Linosa, but *Stenosis brignonei* Koch, 1935 is endemic to Linosa and Lampedusa. The tenebrionid fauna of the Maltese Islands includes nine or ten endemic taxa. Moreover, the Maltese population of *Stenosis melitana* Reitter, 1894, formerly thought to be endemic but also found relatively recently in southern Sicily, could still represent a distinct form.

## CONCLUSIONS

This study investigated the influence of island geographical and environmental (landscape) features on three main, intercorrelated biogeographical patterns: species richness, species assemblage composition and inter-island faunal similarity of tenebrionid beetles on 25 islands around Sicily. These three patterns were regulated by different factors. Species richness, which does not take into account species identities, was mostly influenced by island area and landscape heterogeneity. When species identities were considered, no substantial effect of landscape was detected. Tenebrionids are detritivorous and most species can exploit a number of different biotopes in several kinds of land cover categories. Thus, most species can probably exploit biotopes across a variety of land-cover categories. This low environmental specialization brings about low influence of landscape on species assemblage composition, whereas greater landscape heterogeneity supports larger species numbers.

Current isolation does not show a strong influence on species richness, but has a distinct effect in determining species assortments on the remotest islands. Historical factors, i.e. Pleistocene landbridge connections, are not detectable in species richness relationships with geographical variables or in assemblage gradients, but emerge distinctly from inter-island similarities. Thus, the results presented in this study show that the same geo-

graphical or environmental gradient may have very different effects on different aspects of species distributions and multiple approaches are needed for understanding multiple biogeographical patterns.

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APPENDIX 1. Presence (1) / absence (0) of tenebrionid beetles on the circum-Sicilian islands. Island numbers as in Table 1. Nomenclature follows Löbl & Smetana (2008). Numbers in square brackets refer to the references listed below. \* = single island endemic; \*\* = taxon endemic to an archipelago within the circum-Sicilian islands; ? = uncertain identification.

Species	Islands																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
* <i>Erodius auduini destefanii</i> [2, 4, 6, 24, 25]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Erodius siculus siculus</i> [1, 2, 6, 8, 11, 16, 19]	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Erodius siculus neapolitanus</i> [2, 5, 6, 16, 19, 33]	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
** <i>Erodius siculus melitensis</i> [16, 19, 26, 36, 37]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
<i>Pachychila frioli</i> [2, 5, 6, 19]	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pachychila crassicollis cossyrensis</i> [2, 4, 6, 12, 17, 19, 43]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Pachychila dejeani dejeani</i> [2, 5, 6, 8, 9, 11, 19, 21, 33, 34, 42]	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
* <i>Pachychila dejeani doderoi</i> [2, 4, 6, 12, 24, 32]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Pachychila tazmaltensis</i> [2, 4, 6, 17, 19, 24]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Tentyria laevigata laevigata</i> [1, 2, 5, 6, 11, 13, 15, 19, 33, 39]	1	0	1	1	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
** <i>Tentyria laevigata leachi</i> [14, 19, 26, 35, 36]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
<i>Tentyria grossa grossa</i> [1, 2, 4, 5, 6, 8, 9, 11, 19, 20, 21, 25, 26, 33, 36, 40, 42]	1	1	1	1	1	1	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0
* <i>Tentyria grossa angustata</i> [2, 6, 12, 43]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Tentyria grossa sommierj</i> [2, 4, 6, 12, 24]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Tentyria latreillei oblongipennis</i> ? [2, 4, 6, 24]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Imatismus villosus</i> [2, 4, 6, 12, 17, 19, 24]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
** <i>Stenosis brignonei</i> [2, 4, 6, 12, 19, 24, 31]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
<i>Stenosis freyi</i> [2, 6, 26, 31, 33, 36]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Stenosis intermedia</i> [2, 5, 6, 11, 19, 21, 33]	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stenosis melitana</i> [14, 17, 19, 26, 31, 35, 36]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
<i>Stenosis sardo sardo</i> [2, 4, 5, 6, 8, 11, 12, 24, 33, 34, 36, 43]	1	1	0	0	1	1	0	0	0	0	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0
** <i>Stenosis schembrii</i> [14, 26, 36]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
<i>Dichillus subtilis</i> [3, 5, 6]	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Dichillus pertusus</i> [2, 4, 6, 8, 11, 19, 26, 36, 43]	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0
<i>Eutagenia aegyptiaca tunisea</i> [2, 4, 6, 17, 24]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Microtelus lethierryi</i> [2, 4, 6, 17, 19, 24]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Elenophorus collaris</i> [2, 5, 6, 19, 26, 33, 36, 38]	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

<i>Alphasida grossa grossa</i> [1, 4, 5, 6, 7, 8, 11, 12, 19, 31, 33, 34, 42, 43]	1 1 0 1 0 0 1 0 0 1 1 0 1 1 1 1 1 0 0 0 0 0 0 0 0
** <i>Alphasida grossa melitana</i> [19, 26, 36]	0 1 1 1 0 1
* <i>Alphasida puncticollis tirellii</i> [2, 4, 6, 12, 19, 24, 31]	0 1 0 0 0 0
* <i>Alphasida puncticollis moltonii</i> [2, 4, 6, 12, 24]	0 1 0 0 0 0
* <i>Asida minima</i> [2, 4, 6, 19, 24, 31]	0 1 0 0 0 0
** <i>Machlopsis doderoi</i> [2, 4, 6, 19, 24, 31]	0 1 1 0 0 0
<i>Sepidium siculum</i> [2, 4, 6]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
<i>Akis spinosa spinosa</i> [2, 5, 6, 11, 19, 42]	0 0 0 0 0 1 1 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0
<i>Akis spinosa barbara</i> [2, 4, 6, 12, 24, 32, 43]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0
<i>Akis subterranea</i> [1, 5, 6, 8, 9, 11, 18, 19, 26, 31, 33, 34, 36]	1 0 1 0 0 1 1 0 0 0 0 0 1 1 1 1 0 0 0 0 1 1 0 0 1
<i>Scaurus aegyptiacus</i> [2, 6, 8, 11, 33, 36]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0
<i>Scaurus tristis</i> [2, 4, 5, 6, 8, 11, 12, 14, 19, 24, 26, 33, 34, 36, 42]	1 1 0 1 0 1 1 0 0 0 0 0 1 1 1 0 0 1 0 1 1 1 1 0 0
<i>Scaurus atratus</i> [2, 4, 5, 6, 9, 11, 12, 19, 32, 33, 43]	1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0
<i>Scaurus striatus</i> [1, 2, 4, 5, 6, 8, 9, 11, 12, 14, 19, 22, 24, 26, 33, 34, 36, 42]	1 1 1 1 1 1 1 0 1 1 0 1 1 1 1 0 0 1 0 1 1 1 1 1 0
<i>Trachyderma lima</i> [2, 4, 6, 19, 26, 36]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0
<i>Pimelia grossa</i> [2, 6, 15]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
<i>Pimelia rugulosa</i> s.l. [1, 2, 5, 6, 8, 9, 11, 19, 20, 21, 25, 33, 34, 35]	1 1 1 1 1 1 1 0 1 1 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0
** <i>Pimelia rugulosa melitana</i> [26, 36]	0 1 1 0 0
<i>Blaps gigas</i> [1, 2, 4, 5, 6, 8, 11, 12, 14, 19, 24, 26, 33, 34, 36, 43]	1 1 1 1 1 1 1 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 1 1 0
<i>Blaps gibba</i> [2, 4, 5, 6, 9, 11, 19, 30, 32, 33, 42, 43]	1 1 1 1 0 1 0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 0 0 0 0
<i>Blaps mucronata</i> [1, 2, 5, 6, 8, 9, 11, 19, 26, 33, 34, 36]	1 0 1 1 1 1 0 0 0 0 0 0 1 1 1 1 0 0 0 0 1 0 0 0 0
<i>Blaps lethifera</i> [2, 6, 8, 11, 19]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0
<i>Blaps nitens</i> [2, 4, 6, 19, 24]	0 1 0 0 0 0
<i>Dendarus lugens</i> [2, 5, 6, 19, 22, 26, 33, 36]	0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 1 0 0
<i>Heliopathes avarus avarus</i> [2, 4, 6, 11, 12, 19, 24, 34, 36]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 1 0 0 0 0
* <i>Heliopathes avarus donatellae</i> [2, 4, 6, 11, 12, 17, 43]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0
* <i>Heliopathes avarus dwejnensis</i> [44]	0 1 0 0 0
<i>Pedinus helopioides</i> [2, 5, 6, 19, 33]	1 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
<i>Pedinus siculus</i> [5, 6]	0 0 0 0 1 0
<i>Pedinus ionicus</i> [2, 6]	0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0
<i>Pedinus punctatostratus</i> [2, 6, 11, 19, 33, 34]	0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0
<i>Dilamus planicollis</i> [2, 6, 19]	0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0
<i>Cheirodes brevicollis</i> [2, 4, 6, 24, 26, 36, 37]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0
<i>Cheirodes sardous sardous</i> [2, 4, 5, 6, 24]	1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0
<i>Allophylax picipes picipes</i> [1, 5, 6, 8, 11, 19, 20, 33, 34]	1 1 1 0 1 1 1 1 1 1 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0
** <i>Allophylax picipes melitensis</i> [14, 19, 26, 36]	0 1 1 1 1
<i>Allophylax costatipennis costatipennis</i> [2, 4, 6, 12, 17, 19, 24]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0
* <i>Allophylax costatipennis godenigoi</i> [2, 6, 11, 17]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
<i>Cnemeplatia atropos</i> [36]	0 1 0 0 0
<i>Gonocephalum obscurum obscurum</i> [1, 2, 4, 5, 6, 11, 12, 19, 24, 33, 34, 43]	1 0 1 0 1 0 1 0 0 0 0 0 0 1 1 0 1 1 0 1 0 1 0 0 0
<i>Gonocephalum granulatum nigrum</i> [2, 5, 6, 8, 11, 19, 34]	1 1 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0
<i>Gonocephalum perplexum</i> [2, 4, 6, 13, 17, 24, 43]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0
<i>Gonocephalum rusticum</i> [2, 3, 4, 5, 6, 11, 19, 24, 26, 33, 36]	1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 1 0 1 1 0 1 1 1 0 0
<i>Gonocephalum setulosum setulosum</i> [2, 4, 5, 6, 12, 19, 24, 26, 36]	1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 0 0
<i>Gonocephalum assimile</i> [6, 24]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0
<i>Opatrum emarginatum</i> [14, 26, 36]	0 1 0 0 0
<i>Opatrum verrucosum</i> [2, 3, 5, 6, 19, 33]	1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
* <i>Opatrum melitense</i> [36]	0 1 0 0 0
* <i>Opatrum validum marcuzzii</i> [2, 6, 17, 20, 33]	0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0
<i>Opatrum validum schlicki</i> [2, 4, 6, 12, 17, 19, 20, 43]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
* <i>Opatrum validum rottembergi</i> [2, 4, 6, 12, 24]	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0
<i>Opatrum obesum</i> [2, 5, 6, 19, 21]	0 1 0
<i>Opatroides punctulatus punctulatus</i> [1, 2, 4, 6, 8, 11, 12, 19, 24, 26, 33, 34, 35, 36, 41, 43]	0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 0 0 1 1 0 0 0
<i>Ammobius rufus</i> [2, 4, 5, 6, 19, 24, 26, 33, 36, 37]	0 1 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0
<i>Clitobius ovatus ovatus</i> [2, 6, 19, 26, 36, 37]	0 1 1 0 0 0
<i>Trachyscelis aphodioides</i> [2, 4, 5, 6, 17, 19, 21, 24, 26, 36, 37]	0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0



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