Calling for a new strategy to measure environmental (habitat) diversity in Island Biogeography: a case study of Mediterranean tenebrionids (Coleoptera: Tenebrionidae)

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Abstract
Many recent researches in island biogeography attempted to disentangle the effects of area *per se* and "habitat diversity" on species richness. However, the expression "habitat diversity" in this context should be avoided, because habitats can be only recognized by referring to the resources needed by a particular species. What is really measured in such researches is some form of "environmental heterogeneity". Although habitat heterogeneity can be measured in various ways, most researches in island biogeography simply used the number of biotopes (typically classified as land cover categories). However, not all biotopes have the same surface.On the basis of the area occupied by each land cover category, it is possible to calculate indices of environmental diversity, evenness and dominance, as commonly done in community ecology research. These indices can be used to investigate the role of environmental diversity in determining species richness. We used the tenebrionid beetles inhabiting twenty-five small islands around Sicily (Central Mediterranean) to illustrate these concepts. We found that both area *per se* and environmental heterogeneity contributed to determine species richness. Moreover, we found that the relationship between species richness and environmental homogeneity followed a power function model. This indicates that environmental homogenization may determine a rapid, non linear decline in species richness.

Key words: diversity, environmental heterogeneity, evenness, habitat hypothesis, structural equations, Sicily.

Introduction

The species-area relationship, i.e. the law modelling how the number of species in a community increases with area, is one of the best documented patterns in island ecology (Whittaker et al. 2008, Whittaker & Triantis 2012, Triantis et al. 2012). Larger islands may host more species because they provide larger targets for dispersing individuals and, since they can support larger populations, the extinction rates for individual species become lower (MacArthur & Wilson 1967, Ricklefs & Lovette 1999; Whittaker & Fernández-Palacios 2007). However, since also the extent and variety of resources a species can use increase with area, one could not exclude that resource availability, and not area, is the key to species coexistence (Rosenzweig 1995, Ricklefs & Lovette 1999). This additional explanation is known as the "habitat diversity" hypothesis, and has received great attention in several recent studies (e.g., Triantis et al. 2005, 2006, Hortal et al. 2009, 2013 for reviews). However, most of them have highlighted various problems in unraveling the "area *per se*" and "habitat di-

versity" hypotheses and the best analytical procedures to test their (relative) magnitude.

In this paper, we describe a comprehensive framework to deal with these issues, focusing on a group of island insects as a case study.

What is a habitat?
The expression "habitat diversity" refers to the idea that a region can be partitioned into a number of habitats, and that each of them can be occupied by a subsample of the total number of species living in the region as a whole. Larger areas are more likely to host more habitats, and hence more species.

Actually, many authors describe habitats in terms of environmental features occurring in specific areas (e.g., number of plant associations, number of soil types, vegetation structure, land-uses, climate, etc.). The concept of habitat has been defined in various and contrasting ways. For example, Dennis (2010) lists nine different definitions given between the 1960s and the 2000s. According to the Dictionary of Ecology (Allaby 2010), the habitat is "The

living place of an organism or community, characterized by its physical or biotic properties". Thus, a habitat can be only recognized by referring to the resources needed by a particular species or to a group of species requiring similar sets of resources (Dennis 2010, Dennis et al. 2003, 2014). Thus, "habitat diversity" is an intrinsically ill-formulated concept, at least as used in current ecological literature, and should not be used to qualify general features of areas. A more appropriate expression to be used in lieu of "habitat diversity" would be "environmental heterogeneity" (see Looijen 1998, Hortal et al. 2013, Stein & Kreft 2014), because it refers to the variety of environmental aspects that may characterize an area.

What is categorized?
We said that larger areas can host more species because they tend to provide organisms with more places where to find necessary resources in quality, quantity and stability. One of the most commonly measures of "habitat diversity" is the number of biotopes (e.g., Kohn & Walsh, 1994, Ricklefs & Lovette 1999), which can be considered a very basic measure of environmental heterogeneity. While habitats exist only in relation to a species, recognition of biotopes is rooted to a particular place, and is therefore appropriate to study if species richness increases with extent and variety of resources. Biotope, as in the case of a habitat, has also been described in different ways. Some definitions of biotope relate it to habitat and the two words are frequently treated as being synonymous (see Dennis 2010; Dennis et al. 2014). In fact, the two variable terms habitat and biotope describe very different phenomena. Habitat, defined as that collection of resources and conditions that ensures the persistence of a population at a site (resource-based definition), is a species-specific term and can be a very complex physical construct. By contrast, biotope, defined as a region (area, space) that is distinguished by particular environmental conditions, is a community-specific term and is a relatively simpler concept to apply. For this reason, biotopes are frequently used as surrogates for habitats, although this can be dangerous, because dimensions of the biotope may exceed that of the habitat space or it may fail to embrace all of resources and conditions needed by a species (see Dennis et al. 2014).

Although a big effort has been spent to reach some consensus for the recognition of broad biotope types (e.g., the European Corine Land Cover classification), definitions and identification criteria of biotopes still vary considerably among different studies. For examples, biotopes have been identified in terms of land cover categories, landscape units, vegetation types, soil types, etc. depending on the spatial scale and on the target taxon. Biotopes are not the only aspect of the environment that can be used to define environmental heterogeneity. Variability of edaphic and climatic factors, elevational ranges within geographical units (e.g. cells or islands), precipitation and temperature ranges, depth of litter, size of rocks, type of substrates, etc. can all determine environmental heterogeneity (Solem et al. 1981, Ricklefs & Lovette 1999, Schoener et al. 2001, Kocher & Williams 2000, Stein & Kreft 2014). The choice is not trivial, and will necessarily vary according to data availability, and to the hypotheses being tested in a particular study.

What is measured?
Most studies dealing with "habitat diversity" tend to indicate the number of biotopes as the "number of habitats". When using biotopes to measure environmental heterogeneity, usually ecologists focus on their number. However, this approach may not be the best choice. For example, it does not consider the relative extent of different biotopes, an aspect that can be of fundamental importance in sustaining viable populations. In addition, two areas may host the same number of biotopes, but they might differ in the relative area and spatial arrangement of these biotopes, thus determining different levels of environmental heterogeneity. Thus, some authors have used a "habitat diversity index" (HD) which takes into account the relative area covered by each "habitat" (= biotope) thus weighting the relative contribution of each biotope (e.g. Ricklefs & Lovette 1999, Fox & Fox 2000). Advances made in the field of community ecology could be helpful to this purpose. It has been long recognized that species number cannot fully describe the diversity of a community. For this, ecologists use a set of indices to quantify diversity, not only in terms of richness but also in terms of species dominance and evenness (equitability). Most of these indices are not specific for biological communities, but can be also applied to quantify environmental diversity, dominance and evenness. Yet, up to date, this idea has been little pursued in biogeographical research and the number of biotopes still remains the most widely used measure of environmental diversity (see Fattorini 2006a; Tognelli & Kelt 2004, Triantis et al. 2005, 2006, Hortal et al. 2009, and references therein). Shannon index (or its modifications) is commonly used in landscape ecology (see Farina 1998, Luoto et al. 2001, Burel & Baudry 2003, Dušek & Popelková 2012 for a discussion) and, less frequently, in biogeography (Lobo & Martín-Piera 2002, Nogués-Bravo & Martínez-Rica 2004, Stefanescu et al. 2004, Maes et al. 2005). However, there are several other 'neglected' indices developed in community ecology which could provide important information to quantify environmental diversity in biogeographical analyses.

The expression "environmental diversity" has been sometimes used as synonym of "habitat diversity" (e.g. Triantis et al. 2005, 2006), and the use of "habitat diversity" has been defended on the basis of its relatively wide use (Panitsa et al. 2006). Like for species richness, also "environmental diversity" can be better expressed in terms of richness, evenness and dominance. Thus, a more general expression, such as "environmental heterogeneity" would be preferable (considering that dominance indi-

cates, in practice, a reduction in heterogeneity). Alternatively, one could use a specific terminology, such as "environmental diversity", "environmental dominance", or "environmental evenness", depending on what is being measured (see also Stein & Kreft 2014 for a review of the use of various expressions).

The case study
To put in practice our observations, we present here a case study in the field of island biogeography dealing, in particular, with the distribution of tenebrionid beetles on the islands surrounding Sicily. Sicily is the largest Mediterranean island, and it is surrounded by a number of small islands, collectively known as the "circumsicilian" islands. The biogeography of the circumsicilian islands is particularly complex (e.g. Fattorini 2010, 2011a,b, and references therein), because they vary greatly in terms of area (Malta, the largest island, has an area of 245.7 km², but most of the islands are below 30 km²), ecological and climatological settings, geological origin (volcanic vs. sedimentary), paleogeography (some were connected to Sicily or Africa during Pleistocene glaciations, others remained isolated) and distance to two different main sources of colonization (Sicily vs. Africa) showing high degree of biotic diversification. Thus, they represent a good model to explore the influence of many possible abiotic determinants on animal communities including environmental heterogeneity. In general, the fauna of these islands is also relatively well known. Among insects, one of the best investigated groups is the beetle family of Tenebrionidae. Thanks to their low dispersal ability, tenebrionids represent excellent biogeographical markers of historical processes and they have been repeatedly used to investigate the biogeography of Mediterranean islands (e.g., Fattorini 2002a,b, 2006a,b,c, 2007a,b,c,d, 2009a,b, 2010, 2011a,b, Fattorini & Fowles 2005, Fattorini et al. 1999, Hausdorf & Hennig 2005, Trichas et al. 2008, Papadopoulou et al. 2008, 2009, 2010), including the circumsicilan ones (Fattorini 2010, 2011a,b).

Material and methods

Study area
We used data from 25 circumsicilian islands, including: the Aeolian Islands (volcanic: Stromboli, Panarea, Vulcano, Lipari, Salina, Filicudi, Alicudi, and seven smaller islets), the Egadi Islands (sedimentary: Levanzo, Favignana, Marettimo), the Pelagie (Linosa, volcanic, and Lampedusa and Lampione, sedimentary), and the Maltese Islands (Malta, Gozo, Comino, Cominotto, and Filfla, sedimentary); Ustica and Pantelleria (both volcanic), are rather isolated. For detailed information on these islands see Mazzola et al. (2001), Fattorini (2010, 2011a,b) and Savona Ventura (2011). Data on tenebrionid distribution in the circumsicilian islands were extracted from Fattorini (2011b) and updated with new data reported by Lo Cascio & Pas-

ta (2012) and Lillig et al. (2012a,b). Species presence/absence on individual islands is given in Appendix 1.

Environmental categorization
For an ecological characterization of island landscapes, we calculated the extent of island surface occupied by different land cover categories according to the European Corine Land Cover classification. Although somewhat crude and of limited value for small regions, 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 circumsicilian islands (Italian Ministry of the Environment and Protection of the Territory and Sea 2009, Malta Environment and Planning Authority 2009). This number of environmental categories is disproportionately large in respect to the small number of islands composing the archipelago. Moreover, some categories are represented by very small patches and can be easily combined into broader categories. Thus, we used the following broader land cover categories: *Built up areas* (including *Continuous urban fabric*, *Discontinuous urban fabric*, *Industrial or commercial units*, *Port area*, *Airports*, *Mineral extraction sites*, *Dump Sites*, *Green urban areas*, and *Sports and Leisure Facilities*), *Cultivations* (including *Vineyards*, *Non-irrigated arable land*, *Natural grassland* [because most often found in areas where there is extensive agricultural activity], *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 land cover units are coarse in comparison to the scale at which insects perceive small-scale environmental heterogeneity, they correspond well to distinct keystone structures (*sensu* 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 2008, 2009c).

Environmental heterogeneity measures
In addition to score the number of land cover categories (N) occurring on each island, we used the land category information to compute various synthetic indices of environmental heterogeneity (Table 1). For this, we applied indices of diversity, evenness and dominance derived from those used in community ecology (Legendre & Legendre 1998, Magurann 1988, 2004, Hayek & Buzas 2010):
- 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

Table 1 – Tenebrionid beetle species richness on the circumsicilian islands, island area, elevation and environmental heterogeneity and homogeneity. **N** = number of land cover categories, **H** = Shannon index; **J** = Pielou equitability (evenness); D_{Mg} = Margalef richness index; **C** = Simpson dominance index; **d** = Berger-Parker dominance.

Island name	Species number	Area (km²)	Elevation (m)	N	H	J	D_{Mg}	C	d
Lipari	32	37.29	602	4	1.352	0.9756	0.285	0.2675	0.3539
Salina	24	26.38	962	3	0.774	0.7046	0.1965	0.5664	0.7273
Vulcano	22	20.87	500	5	1.38	0.8573	0.4022	0.2794	0.3596
Stromboli	25	12.19	926	3	0.9032	0.8221	0.2126	0.4508	0.5769
Filicudi	15	9.49	774	3	0.7826	0.7124	0.2184	0.549	0.7053
Alicudi	18	5.1	675	3	0.878	0.7992	0.2343	0.4633	0.5882
Panarea	22	3.34	421	3	0.991	0.9021	0.2465	0.4105	0.559
Basiluzzo	3	0.29	165	1	0	0	0	1	1
Lisca Bianca	4	0.0413	30	1	-0.00734	0	0	1.015	1
Bottaro	7	0.0073	21	1	-0.04376	0	0	1.088	1
Scoglio Faraglione	4	0.0049	35	1	-0.2486	0	0	1.501	1
Pietra del Bagno	3	0.0021	21	1	-0.05123	0	0	1.103	1
Ustica	26	8.6	238	5	1.453	0.9029	0.4415	0.2634	0.3644
Levanzo	18	5.61	278	2	0.4702	0.6784	0.1158	0.7059	0.8208
Favignana	28	19.7	302	3	0.7316	0.6659	0.2023	0.5611	0.7038
Marettimo	16	12.06	686	3	0.5284	0.481	0.2128	0.7312	0.848
Pantelleria	23	86	591	5	1.088	0.6759	0.352	0.4206	0.5935
Linosa	19	5.34	195	3	0.9563	0.8705	0.233	0.4323	0.5837
Lampione	6	0.025	40	1	0	0	0	1	1
Lampedusa	28	20.2	133	4	1.107	0.7983	0.3026	0.384	0.5299
Malta	46	246	253	7	1.089	0.5599	0.4834	0.3906	0.5152
Gozo	27	67	190	4	1.023	0.7379	0.27	0.3854	0.4397
Comino	11	3.5	70	1	0	0	0	1	1
Cominotto	2	0.25	8	1	0	0	0	1	1
Filfla	3	0.06	60	1	0	0	0	1	1

A is the total surface of the island. *C* varies from 0 (all land cover categories have equal extent) to 1 (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 (one land cover category dominates the landscape completely) to high values for landscapes with many categories, each with a small extent.

- Pielou equitability (evenness): $J = H/\ln N$.
- Margalef richness index: $D_{Mg} = (N - 1)/\ln(A)$.
- Berger-Parker dominance: $d = A_{max}/A$, i.e. the extent of the dominant land cover category (A_{max}) divided by *A*.

As a further measure of environmental heterogeneity we used island maximum elevation. Elevation is correlated with temperature, precipitation, humidity, wind speed, evaporation and insolation, so it has been claimed to be a measure of "habitat" diversity (Newmark, 1986). Moreover, regression studies often find altitude to be an important variable in explaining species numbers on islands, in

some cases ranking only second to, or even ahead of, island area (Biondi 1995, Whittaker & Fernández-Palacios 2007). Moreover, according to the General Dynamic Model of island biogeography, island elevation is related to island geological dynamics and evolution, peaking in islands whose environmental heterogeneity is at maximum (Whittaker et al. 2010).

Disentangling the effects of area and environmental heterogeneity

As environmental heterogeneity and area tend to be interrelated, it is very difficult to disentangle their different contribution in determining species richness. Several studies aimed at testing the relative importance of area and environmental heterogeneity (under the rubric of "habitat diversity") in island biogeography have used structural equation models (e.g., Kohn & Walsh 1994, Hausdorf & Hennig 2005, Fattorini 2006a, Triantis et al. 2005, 2006, Karels et al. 2008, Ames et al. 2012, Cabral et al. 2014). Structural equation models (which include procedures also known as "path analysis") allow the relative direct and

indirect effects of casual (or predictor) variables to be assessed according to an *a priori* model under several assumptions (Grace & Pugesek 1998, Grace 2006). The appropriate structural equation model for the effect of area and environmental heterogeneity upon species per island is shown in Fig. 1a. The coefficients a_1, b_1 and b_2 represent direct effects of one variable on another; a_1 is the simple correlation coefficient for the variables environmental heterogeneity and area as obtained from the regression $lnEH = alnA + c$; b_1 and b_2 are the standardised regression coefficients from the multiple regression model $lnS = alnA + blnEH + c$. Indirect effects are calculated as the product of the coefficients along the links between causal variables and the response variable through other causal variables. Effect coefficients are the sum of direct and indirect effects. The species-area relationship is best modelled by the power function ($S = cA^z$), where S is species number, A is area, and c and z are fitted parameters (Drakare et al. 2006, Martín & Goldenfeld 2006, Fattorini 2006b, 2007b, Dengler 2009, Triantis et al. 2012). In all multiple regression models, we linearized power functions by logarithmic transformation: $lnS = lnc + zlnA$. Because some environ-mental indices had 0 values, we used $ln(x+1)$ transformations in all instances.

Results

Area was an important correlate of species richness and the species-area relationship (SAR) was well modeled by a power function ($lnS = [2.356 \pm 0.094] + [0.243 \pm 0.028]lnA$; $R^2 = 0.763$, $F_{(1,23)} = 74.104$, $P < 0.00001$; Figure 2). Species richness was also strongly correlated with all measures of environmental heterogeneity (i.e., diversity and evenness) (positively) and homogeneity, i.e. dominance (negatively) (Spearman rank correlation coefficients significant at $P < 0.05$ after Bonferroni sequential corrections with $k = 7$; Table 2). All measures of environmental heterogeneity were positively correlated with island area, whereas those of environmental homogeneity had a negative correlation (Spearman rank correlation coefficients significant at $P < 0.05$ after Bonferroni sequential corrections with $k = 7$; Table 2).

When different functions were applied to search for
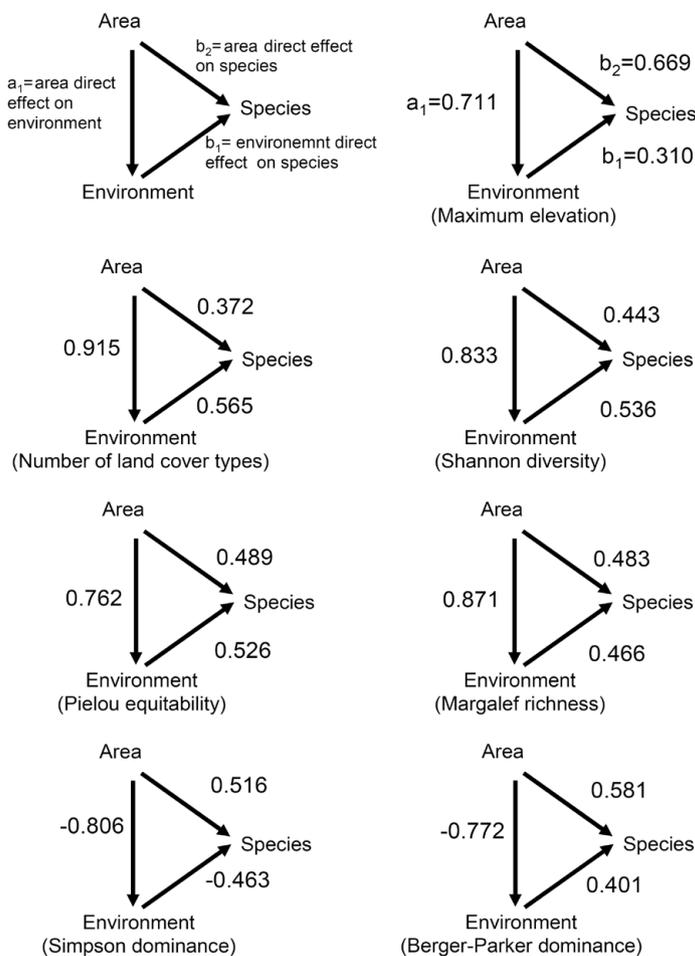
Fig. 1 – Path models of species richness as a function of area and environmental heterogeneity or homogeneity. All variables were $ln(x+1)$ transformed.
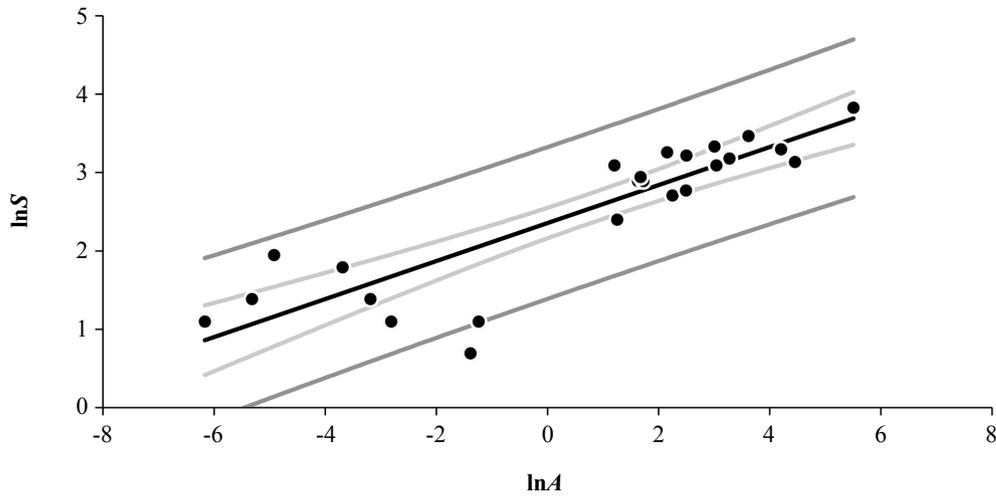
Fig. 2 – Regression of number of species (ln$S$) against island area (ln$A$, in km^2). Light grey lines: 95% confidence intervals. Dark grey lines: 95% prediction intervals.

the best fit models for species richness and environmental heterogeneity or homogeneity, we found that, in general, a power function explained a larger fraction of variance (R^2 comprised between 0.617 and 0.821) than linear models (R^2 comprised between 0.221 and 0.824), except in the case of Margalef richness and number of land cover categories, where the two models explained virtually identical percentages of variance ($R^2 = 0.792$ for the linear model and $R^2 = 0.787$ for the power model of Margalef index; $R^2 = 0.824$ for the linear model and $R^2 = 0.821$ for the power model of number of land cover categories), and Berger-Parker dominance, where the linear model explained a slightly larger percentage of variance ($R^2 = 0.720$) than power model ($R^2 = 0.708$).

Results of structural equation models are shown in Fig-

ure 1. All coefficients reported in the graphs were significant at $P < 0.05$, except b_2 in the pathway obtained for number of land cover categories, which indicates that, in this particular case, the contribution given by environmental heterogeneity virtually obliterated the effect of area.

When maximum elevation was used as a measure of environmental heterogeneity, the magnitude of the indirect effect of area ($a_1 b_1$) on species per island was much lower than its direct effect (b_2). The direct effect of area (b_2) on species richness greatly exceeded the direct environment effect on species (b_1), but the total effect of area, when direct and indirect effects are summed ($a_1 b_1 + b_2$), was much greater (2.9 times larger) than the effect of environment.

For Shannon index, Pielou equitability and Margalef richness, the magnitude of the indirect effect of area ($a_1 b_1$) on species per island was roughly similar to (Shannon) or lower to (Pielou and Margalef) its direct effect (b_2). Using these indices, the direct effect of environment (b_1) on species richness exceeded the direct area effect on species (b_2), but the total effect of area, when direct and indirect effects are summed ($a_1 b_1 + b_2$), was greater (1.7 times larger) than the effect of environment.

For the two indices of dominance (Simpson and Berger-Parker) the indirect effect of area on species per island was substantially lower than its direct effect. The direct effect of environmental heterogeneity on species richness was lower than the direct area effect on species, but the total effect of area, when direct and indirect effects were summed, was about twice the effect of environmental heterogeneity.

Finally, when the number of habitats was considered, the indirect effect of area ($a_1 b_1 = 0.517$) on species per island was substantially higher than its direct effect ($b_2 = 0.372$). The direct effect of environmental heterogeneity ($b_1 = 0.565$) on species richness exceeds the direct area effect on species ($b_2 = 0.372$), but the total effect of area,

Table 2 – Spearman rank correlation coefficients (r_s) of species richness and area with environmental variables. **N** = number of land cover categories, **H** = Shannon index; **J** = Pielou equitability (evenness); **DMg** = Margalef richness index; **C** = Simpson dominance index; **d** = Berger-Parker dominance. **P** = probability.

	Species		**Area**	
	r_s	P	r_s	P
Area	0.854	<0.00001		
Elevation	0.588	<0.002	0.693	0.0001
N	0.871	<0.00001	0.883	<0.00001
H	0.831	<0.00001	0.816	<0.00001
J	0.734	<0.00001	0.602	<0.00001
D_{Mg}	0.826	<0.00001	0.802	<0.00001
C	-0.841	<0.00001	-0.799	<0.00001
d	-0.873	<0.00001	-0.777	<0.00001

when direct and indirect effects were summed ($a_1b_1+b_2 = 0.889$), was greater (1.57 times) than the effect of environmental heterogeneity (b_1), although less markedly than for the aforementioned indices of diversity or evenness.

In summary, the use of various measures of environmental heterogeneity led to different results as regards the importance of direct and indirect effects of area. However, although the total effect of area was invariably greater than the effect of environmental heterogeneity, area exerts from 24.7 to 58.1% of its overall effect on species number through a powerful effect on environmental heterogeneity/homogeneity, which indicates that environmental heterogeneity is actually important in determining tenebrionid diversity. Yet, the direct influence of area on species richness was higher than the direct effect of environment when maximum elevation and dominance indices were used, it was similar when Margalef richness index was used, and it was lower when diversity or evenness indices were used, and it was much lower when number of land cover was used.

Discussion

Many studies attempted to assess the importance of environmental heterogeneity in explaining variations of species richness in different areas and animal groups (e.g., Buckley 1982, Rafe et al. 1985, Deshaye & Morisset 1988, Kohn & Walsh 1994, Tjørve 2002). However, most of these researches are hampered by two main problems: first, habitat requirements may differ enormously among species; second, there is no consensus among ecologists about the definition and recognition of habitats (Rosenzweig 1995, Hall et al. 1997, Dennis et al. 2003). The latter problem is largely a reflection of the first one, because habitats can be defined, and hence recognized, only with reference to species, with each species having its own habitat. Moreover, a given guild may have very specific environmental requirements but select slightly differentiated micro-biotopes, so that habitat categorization may have to be adapted accordingly (such as in the case of peculiar cases, as those of canopy and cave animals).

We agree in the use of the word "habitat" to indicate the resources used by a species as recommended by Dennis and coworkers (Dennis 2010; Dennis et al. 2003, 2014), and propose to use "environmental heterogeneity" instead of "habitat diversity" to express the environmental complexity of an area and to any kind of variability in environmental characteristics that can affect species presence. This includes the range of environmental conditions (which can include number of biotopes, landscape units, plant associations, soil types, etc. and their proportional contribution), as well as their spatial configuration, and their variation over time.

While the habitat is a characteristic of the species, these measures of environmental heterogeneity depend on the characteristics of the environment. However, the potential array of features that can be used to express environmental heterogeneity is virtually infinite. Thus, the characteristics to be measured must be reduced to a subset chosen by researchers according to their subjective perception of the environment. Although an enormous variety of environmental characteristics can be easily measured using standardized techniques, this does not imply that every approach to measure environmental heterogeneity is appropriate for every group of organisms. On the other hand, since environmental heterogeneity is measured independently from species requirements, comparing the effects of different measures of environmental heterogeneity on species richness (or other measures of alpha diversity) of a given animal group may help identifying which aspects of the environment are more important for the target species assemblages (e.g. guilds or communities). In the study case presented here, we considered various measures of environmental heterogeneity: maximum island elevation, number of land cover categories, and a series of indices that use the proportional surface extent of land cover categories to express their richness, proportional diversity, evenness and dominance. It is well known that larger islands show higher levels of environmental heterogeneity (Harner & Harper 1976, Rafe et al. 1985, Gibson 1986, Rosenzweig 1995). We confirmed this trend here since all the measures of environmental heterogeneity/homogeneity we used were correlated with island area. A strong link between environmental heterogeneity and area can simply result as a probabilistic phenomenon leading to a more likely occurrence of rare biotopes or landscapes in larger areas (Whitehead & Jones 1969, Kohn & Walsh 1994). The same may hold for other environmental categorizations: for example, elevational range, which tends to increase with island area (Fattorini 2002a,b, Steinbauer et al. 2013). Altitude, in turn, determines different climatic levels and high variability in sun exposure, slope, and geological structure. The complex intercorrelation between area and environmental heterogeneity makes it difficult to disentangle the relative importance of these factors in regulating species richness. Typically, structural equation models are suggested as a good statistical way to distinguish the role of multiple collinear variables (such as area and environmental heterogeneity) in respect to various response variables (Sokal & Rohlf 1995, Grace & Pugesek 1997, 1998, Legendre & Legendre 1998, Triantis et al. 2005).

The results of structural equation models for the tenebrionid richness on the circumsicilian islands indicate that the variance in species richness explained by the intercorrelation of area and environmental heterogeneity, and environmental heterogeneity and area separately, vary substantially according to the measure used. When expressed as number of land cover categories, habitat heterogeneity overwhelmed the influence of area, whose influence became statistically not significant, while in all other cases both area and environmental heterogeneity exerted a significant effect. This may suggest that tenebrionid beetles

are more sensitive to the number of land cover categories existing on an island than to their proportional extent. Tenebrionids are usually detritivorous insects, and most species can exploit a number of different biotopes (e.g. under bark or stones, on foliage, into ant, mammal and bird nests, into the sand of river banks and coastal dunes, etc.) in several kinds of land cover categories. Even if land cover categories used in this study are coarse in comparison to the insect scale , each category have different keystone structures (e.g., microclimate conditions, food resources, and soil characteristics). Thus, the number of biotopes that can be used by tenebrionids increases with the number of land cover units, but this effect is only slightly affected by the extent of each land cover unit. This happens because, even when a certain land cover category covers a small surface at the scale of island area, this would still be sufficient to include a good number of biotopes at the scale of the insect. Looking at the percentage of variance in species richness explained by area and number of land cover categories, and the correlation between area and land cover categories, it is clear that the number of land cover categories is highly related to area, but also explains something more for Tenebrionidae. In this respect, the number of land cover categories encompasses all the variance explained by the area as a correlate.

When using indices of proportional richness, diversity, evenness and dominance to express environmental heterogeneity/homogeneity, we found that tenebrionid richness correlated positively with environmental heterogeneity (richness, diversity and evenness), and negatively with environmental homogeneity (dominance). This means that environmental heterogeneity promotes species richness, whereas homogenization has a negative impact. The positive relationship between environmental heterogeneity and tenebrionid richness is also in accordance with the fact that landscape diversity typically leads to an increment in the proportion of generalist insect species (Jonsen & Fahrig 1997, Krauss et al. 2003).

Kadmon and Allouche (2007) suggested that species richness should follow a hump-shaped distribution in relation to increasing biotope numbers ('habitat diversity' according to authors' use). According to this model, species diversity initially increases with number of biotopes, from a very simple island into a biotope-wise more complex island, until a maximum species richness is reached, and then declines because more biotope types reduce the total area of any single biotope type, in turn reducing the suitable biotope for any given species. This model has been however criticized by Hortal et al. (2009, 2013), who, in contrast, found that species richness on islands usually increases with number of "habitats" (=biotopes) and that it never decreases. Results obtained from the tenebrionids of the circumsicilian islands support the findings of Hortal et al. (2009, 2013), not only as regarding for the number of landscape units, but also for the various measures of environmental diversity. However, relationships between species richness and environmental heterogeneity or homogeneity were not linear, as in the models used by Hortal et al. (2009, 2013), but follow a power function model. This indicates that, at least in our study, environmental homogenization may determine a rapid, non linear decline in species richness. These findings may have important implications in conservation biology, which could be better clarified by future research applying our analytical framework to other archipelagos and biota.

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Appendix 1. Presence (1) / absence (0) of tenebrionid beetles on the circumsicilian islands.

Species	Filfla	Cominotto	Comino	Gozo	Malta	Lampedusa	Lampione	Linosa	Pantelleria	Marettimo	Favignana	Levanzo	Ustica	Pietra del Bagno	Scoglio Faraglione	Bottaro	Lisca Bianca	Basiluzzo	Panarea	Alicudi	Filicudi	Stromboli	Vulcano	Salina	Lipari
Accanthopus velikensis (Piller & Mitterpacher, 1783)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Akis subterranea Solier, 1837	1	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1
Akis trilineata trilineata Herbst, 1799	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0
Akis trilineata barbara Solier, 1837	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Allophylax (Allophylax) picipes picipes (Olivier, 1811)	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	1
Allophylax (Allophylax) picipes melitensis (Baudi, 1876)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0
Allophylax (Phylaximon) costatipennis costatipennis (Lucas, 1846)	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allophylax (Phylaximon) costatipennis godenigoi Canzoneri, 1970	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alphasida (Glabrasida) grossa grossa (Solier, 1836)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Alphasida (Glabrasida) grossa melitana (Reitter, 1894)	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Alphasida (Glabrasida) puncticollis moltonii Canzoneri, 1972	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Alphasida (Glabrasida) puncticollis tirellii (Leoni, 1929)	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ammobius rufus (Lucas, 1846)	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1
Asida (Asida) minima Reitter, 1917	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Blaps (Blaps) gibba Laporte de Castelnau, 1840	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Blaps (Blaps) gigas (Linné, 1767)	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1
Blaps (Blaps) lethifera lethifera Marsham, 1802	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
Blaps (Blaps) mucronata Latreille, 1804	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Blaps (Blaps) nitens nitens Laporte de Castelnau, 1840	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Catomus (Catomus) rotundicollis (Guérin-Méneville, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Catomus (Catomus) sp.	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Centorus (Belopus) elongatus ecalcaratus (Seidlitz, 1896)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cheirodes (Cheirodes) sardous sardous Géné, 1839	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheirodes (Pseudanemia) brevicollis (Wollaston, 1864)	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
Clitobius (Clitobius) ovatus ovatus (Erichson, 1843)	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cnemeplatia atropos atropos A. Costa, 1847	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corticeus (Corticeus) bicolor (Olivier, 1790)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Corticeus (Corticeus) unicolor Piller & Mitterpacher, 1783	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cossyphus (Cossyphus) moniliferus moniliferus Chevrolat, 1833	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Crypticus (Crypticus) gibbulus (Quensel, 1806)	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0

11

Species	Filfla	Cominotto	Comino	Gozo	Malta	Lampedusa	Lampione	Linosa	Pantelleria	Marettimo	Favignana	Levanzo	Ustica	Pietra del Bagno	Scoglio Faraglione	Bottaro	Lisca Bianca	Basiluzzo	Panarea	Alicudi	Filicudi	Stromboli	Vulcano	Salina	Lipari
Dichillus (Dichillocerus) pertusus (Kiesenwetter, 1861)	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dichillus (Dichillus) subtilis Kraatz, 1862	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Dilamus (Dilamus) planicollis planicollis Fairmaire, 1883	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Eledona agricola (Herbst, 1783)	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erodius (Erodius) audouini destefanii Failla Tedaldi, 1887	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erodius (Erodius) siculus neapolitanus Solier, 1834	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Erodius (Erodius) siculus melitensis Reitter, 1914	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erodius (Erodius) siculus siculus Solier, 1834	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Eutagenia aegyptiaca tunisea Normand, 1936	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gonocephalum (Gonocephalum) assimile (Küster, 1849)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gonocephalum (Gonocephalum) granulatum nigrum (Küster, 1849)	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1
Gonocephalum (Gonocephalum) obscurum obscurum (Küster, 1849)	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Gonocephalum (Gonocephalum) perplexum (Lucas, 1846)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Gonocephalum (Gonocephalum) rusticum (Olivier, 1811)	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Gonocephalum (Gonocephalum) setulosum setulosum (Faldermann, 1837)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Gunarus parvulus (Lucas, 1849)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Heliopates (Heliopates) avarus avarus Mulsant & Rey, 1854	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Heliopates (Heliopates) avarus donatellae (Canzoneri, 1970)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heliopates (Heliopates) avarus dwejrensis Scupola & Mifsud, 2002	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Helops (Helops) caeruleus caeruleus (Linné, 1758)	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Helops (Helops) rossii Germar, 1817	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Imatismus villosus (Haag-Rutenberg, 1870)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1
Leptoderis collaris (Linné, 1767)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lyphia tetraphylla (Fairmaire, 1856)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Machlopsis doderoi Gridelli, 1930	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microtelus lethierryi Reiche, 1860	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Myrmechixenus picinus (Aubé, 1850)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
Nalassus (Helopondrus) assimilis (Küster, 1850)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Nalassus (Nalassus) aemulus aemulus (Küster, 1850)	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Nalassus (Nalassus) dryadophilus (Mulsant, 1854)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Nalassus (Nalassus) pastai Aliquò, Leo & Lo Cascio, 2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

12

Species	Filfla	Cominotto	Comino	Gozo	Malta	Lampedusa	Lampione	Linosa	Pantelleria	Marettimo	Favignana	Levanzo	Ustica	Pietra del Bagno	Scoglio Faraglione	Bottaro	Lisca Bianca	Basiluzzo	Panarea	Alicudi	Filicudi	Stromboli	Vulcano	Salina	Lipari
Odocnemis (Odocnemis) clypeatus (Küster, 1851)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odocnemis (Odocnemis) ruffoi ruffoi (Canzoneri, 1970)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oochrotus unicolor moltonii Canzoneri, 1961	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Opatroides punctulatus punctulatus Brullé, 1832	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Opatrum (Colpophorus) emarginatum Lucas, 1846	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Opatrum (Colpophorus) validum marcuzzii Canzoneri, 1972	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Opatrum (Colpophorus) validum rotembergi Canzoneri, 1972	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
Opatrum (Colpophorus) validum schlicki Gebien, 1906	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Opatrum (Opatrum) melitense Küster, 1849	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opatrum (Opatrum) obesum Olivier, 1811	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opatrum (Opatrum) verrucosum Germar, 1817	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1
Pachychila (Pachychichilina) dejeani dejeani (Besser, 1832)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pachychila (Pachychichilina) dejeani doderoi Peyerimhoff, 1927	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachychila (Pachychila) crassicollis cossyrensis (Ragusa, 1875)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Pachychila (Pachychila) frioli Solier, 1835	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pachychila (Pachychila) tazmaltensis Desbrochers des Loges, 1881	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paroderus lugens (Mulsant & Rey, 1854)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pedinulus ionicus Kiesenwetter, 1880	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pedinus (Pedinus) helopioides Germar, 1814	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pedinus (Pedinus) punctatostriatus Mulsant & Rey, 1853	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1
Pedinus (Pedinus) siculus Seidlitz, 1893	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pentaphyllus testaceus (Hellwig, 1792)	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Phaleria (Phaleria) acuminata acuminata Küster, 1852	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Phaleria (Phaleria) bimaculata bimaculata (Linné, 1767)	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Phtora (Phtora) crenata Germar, 1836	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pimelia (Pimelia) grossa Fabricius, 1792	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0
Pimelia (Pimelia) rugulosa rugulosa Germar, 1824	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pimelia (Pimelia) rugulosa melitana Reitter, 1915	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Probaticus (Pelorinus) anthrax (Seidlitz, 1896)	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Probaticus (Pelorinus) cossyrensis Sparacio, 2007	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudoseriscius cameroni (Reitter, 1902)	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	Lipari	Salina	Vulcano	Stromboli	Filicudi	Alicudi	Panarea	Basiluzzo	Lisca Bianca	Bottaro	Scoglio Faraglione	Pietra del Bagno	Ustica	Levanzo	Favignana	Marettimo	Pantelleria	Linosa	Lampione	Lampedusa	Malta	Gozo	Comino	Cominotto	Filfla
Pseudoseriscus griseovestis (Fairmaire, 1879)	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
Scaurus aegyptiacus aegyptiacus Solier, 1838	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Scaurus atratus Fabricius, 1775	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Scaurus striatus Fabricius, 1792	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	0	0	1	0	1	1	1	1	0	0
Scaurus tristis Olivier, 1795	1	1	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0	0
Sclerum multistriatum (Forskal, 1775)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sepidium siculum Solier, 1843	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
Stenosis brignonei Koch, 1935	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Stenosis freyi Koch, 1940	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenosis intermedia intermedia (Solier, 1838)	1	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Stenosis melitana Reitter, 1894	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Stenosis sardoa sardoa (Küster, 1848)	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0
Stenosis schembrii Canzoneri, 1979	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tentyria (Tentyria) grossa grossa Besser, 1832	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	0	0
Tentyria (Tentyria) grossa angustata Kraatz, 1896	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
Tentyria (Tentyria) laevigata laevigata Steven, 1829	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Tentyria (Tentyria) laevigata leachi Baudi, 1874	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tentyria (Tentyria) cf. grossa sommieri Baudi, 1874	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tentyria (Tentyria) cf. latreillei oblongipennis Fairmaire, 1875	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Trachyderma (Trachyderma) lima (Petagna, 1819)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Trachyscelis aphodioides aphodioides Latreille, 1809	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0
Xanthomus pallidus (Curtis, 1830)	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
Total	**32**	**24**	**22**	**25**	**15**	**18**	**22**	**3**	**4**	**7**	**4**	**3**	**26**	**18**	**28**	**16**	**23**	**19**	**6**	**28**	**46**	**27**	**11**	**2**	**3**