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Habitat and ecological diversity influences the species-area relationship and the biogeography of the Sicilian archipelago's isopods

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Abstract
Terrestrial isopods are a well-studied invertebrate taxon in Sicily and in the surrounding islands (Maltese archipelago included). During the last 30 years their systematics, ecology and biogeography have been analysed by many authors. The size and the diverse geological origin of the Sicilian archipelago represents an ideal open laboratory in which to study some biogeographical patterns, such as the species-area relationship (SAR). Since many species show limited adaptation to broad physiological conditions and low mobility, and, therefore, their active dispersion is very slow, SAR can be a useful means to examine biogeographical patterns of isopods. Here we analyse their biogeography and whether there is a relationship between the area and the habitat variability of the island surveyed, and whether these factors have an either direct or coupled influence on species richness and ecology. Moreover, we evaluate a potential relationship between Isopoda species richness and the distance from the centre of dispersion (Sicily). Finally, we test for a difference in species and habitat richness between volcanic and non-volcanic islands. Our results show a positive correlation between the area and the habitat, more significant than that between the area and the species, leading us to speculate that habitat diversity has an influence on the SAR of isopods. We find a significantly higher richness of both species and habitats on non-volcanic islands. Finally, our analysis confutes the hypothesis that the number of isopod species on the archipelago's islets declines with the distance from Sicily. We suggest some potential explanations.

Keywords: *Isopoda, Sicily, island biogeography, habitat, species-area curve*

Introduction

Terrestrial isopods are the only taxon of Crustacea adapted to a terrestrial life. Many studies on the systematics, ecology and biogeography of this group have been conducted, and evidence of low mobility and slow dispersion for most of the species has been reported (Vandel 1960). Furthermore, it has been shown that many species have a limited adaptation to broad physiological conditions (i.e. "stenoecy"; Argano & Manicastri 1995; Mazzei et al. 2014).

This taxon has been well studied in Sicily and in the surrounding islands (Maltese archipelago included) during the last 30 years (Caruso et al. 1987; Messina et al. 2011, 2016a,b).

Its extension and diverse geological structure make the Sicilian archipelago an ideal open laboratory in which to study some biogeographical patterns, such as the species-area relationship (SAR).

SAR is one of the best-known and most-studied correlations in ecology (Tjørve & Turner 2009). Measuring how the number of observed species increases upon enlarging the sampled area constitutes a convenient tool to quantify the spatial structure of biodiversity (Messina et al. 2016a; Cazzolla Gatti 2017; Cazzolla Gatti et al. 2017b; Cazzolla Gatti & Notarnicola 2018). Moreover, SAR is an important means to understand the distribution of biological diversity and to predict species extinction (Matthews et al. 2014). The shape of

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the species-area curve is affected by various factors at different scales (Turner & Tjørve 2005). Ecologists have employed SAR to inspect community properties (Cain 1938), to estimate diversity (Plotkin et al. 2000), and to understand the loss of species caused by both habitat fragmentation (Harrison & Bruna 1999) and climate change (Malcolm et al. 2006). The effect of these factors on the curve shape can shed light on the abundance of species and their spatial distribution (Scheiner 2003; Tjørve et al. 2008; Tjørve & Turner 2009; Cazzolla Gatti 2016a,b; Cazzolla Gatti et al. 2017a,c).

Gentile and Argano (2005) found that the Oniscidea fauna from small islands of the Mediterranean Sea is highly structured, with major and minor geographical patterns being identifiable. Their results showed that some, but not all, of Isopoda's biogeographical complexity can be explained by interpreting the different shapes of species-area curves.

The distribution of terrestrial isopods depends on numerous ecological factors, among which the most important are: (i) limestone content of soils; (ii) air humidity; (iii) light and temperature; soil salinity; (iv) vegetation type (Caruso et al. 1987; Pezzino 2014).

The limestone content of soils can limit the number of species in a region: this is probably linked to the demand for calcium carbonate with which these animals impregnate their cuticle. This need, along with numerous other factors, such as the temperature, means that in the Mediterranean regions, where calcareous soils prevail, the number of species of Oniscidea is high, while in regions where the soils are of metamorphic or magmatic nature, their abundance and diversity are much lower (Caruso et al. 1987; Pezzino 2014). Humidity is another limiting factor for terrestrial isopods since the defence mechanisms developed by these animals against desiccation are not always efficient; this is why isopods are always associated with humid environments (Caruso et al. 1987; Pezzino 2014). Isopods are shade-tolerant species and, therefore, more active at night, when the humidity is greater than during the day (Caruso et al. 1987; Pezzino 2014).

Some species (halophilous ones), such as those belonging to the genera *Ligia* or *Tylos*, do not tolerate a low salinity in their environment, because they are not completely freed from their marine origins; and vice versa, most of the species that have a long terrestrial evolution do not tolerate high salinity levels (Argano 1979). Vegetation is another relevant factor that influences terrestrial isopods' distribution, and species are often grouped according to their habitat, such as meadow species, swamp species, forest species, humus species, etc. (Messina et al. 2016b).

Sicily, as it appears today in its insular unity, is relatively recent. In the Paleogene (i.e. in the ancient Tertiary, about 50–70 million years ago), according to Furon (1950), Sicily would have been part of Tirrenide, a large land that emerged in the area occupied by the current Tyrrhenian Sea, of which, together with the Maltese Islands and the coasts of North-West Africa, it would have constituted the southern margin. Northern Sicily would have been united to southern Italy, but separated by a narrow arm of the sea from the oriental coasts (*corso-sarde*) of the Tirrenide, and separated also from the iblea region that remained united to the Maltese Islands and to Tunisia (Pasa 1953). A marine transgression would have subsequently fragmented the Tirrenide, and during the Middle and lower Miocene (about 20–30 million years ago) the north-eastern stretch of the current Sicily, joined to the Calabrian and Apennine ridge and to the ibleo-maltese island, did not remain. During the Pontico, a period of great regression, lands emerged in the area today occupied by the Mediterranean; 12–15 million years ago the Italian peninsula emerged and incorporated northern Sicily; to the west the Iberian peninsula stretched eastward beyond the Balearics and between these two territories a third wide area connected the Sardinian-Corsican system to southern France. The two shallow sea arms that separated these three territories were probably occupied by systems of islands and archipelagos. During the ancient Pliocene (10–12 million years ago), the lands that had emerged during the Pontico fragmented and shrank, and Sicily was formed by two separate islands that did not contact the lands nearby: an island to the north made up of northern Sicily and one to the south, limited to the present iblea area. Subsequently, in the course of the Pliocene regression, the area between these two islands progressively emerged and at the beginning of the Quaternary, about 800–500 thousand years ago, a connection between the two islands was made (La Greca 1961). During the Great Glaciation (Roman regression) the emerged lands were enormously increased and at that time Sicily became a unit connected to the east with Calabria and to the south with the Maltese Islands, while in the south-west it extended considerably towards Africa but remained separated from Tunisia by a very narrow channel. During the Würmian, emerged lands around Sicily were smaller, although they were more extensive than the current ones: there was no longer a connection with Calabria and the Maltese islands, but the current shallow waters of the Tunisian channel had emerged and were connected with Sicily. During the Mindel-Riss and Riss-Würm interglacial periods, the

geography of Italy and Sicily became close to its current condition (La Greca & Sacchi 1957). These geological dynamics have surely influenced the terrestrial isopod distribution of the Sicilian archipelago, together with their climatic and ecological adaptations.

The Sicilian archipelago's climate is generally the Mediterranean, with hot summers and mild and rainy winters, and very variable middle seasons. On the coasts, especially the south-western one, the climate is influenced more by African currents so that summers can be very hot. Rainfall on Sicily is not abundant (the annual regional mean is about 633 mm) and is concentrated in the late autumn and early spring (Pezzino 2014). Annual average temperatures are relatively high. For instance, in the Aeolian Islands, the annual average temperature varies between 16 and 30°C (Pezzino 2014). The Aeolian Islands constitute a volcanic system of the Sicilian archipelago formed by the subduction of the oceanic lithosphere below the continental one. This causes lithosphere fusion with the liberation of magma, which at the surface forms an insular arch, the Aeolian arch, 200 km long, composed, besides the seven volcanic emerged islands, by submarine mountains (Pezzino 2014).

The Aeolian Islands, together with Ustica, the Egadi Islands, the Pelagie Islands, Pantelleria and the Maltese Archipelago, constitutes the set of small islands interconnected with the main island, Sicily, and characterised by a rich Mediterranean vegetation (see Table I for habitat characterisation of each island considered in this study).

Here we analyse whether there is a relationship between the area size and the habitat variability of the Sicilian archipelago's islands and whether these factors have a direct or coupled influence on species richness and ecology. Then, we evaluate a potential relationship between Isopoda species richness and distance from the centre of dispersion (Sicily). Finally, we check for the existence of a significant difference in species and habitat richness between volcanic and non-volcanic islands.

Materials and methods

Data set

Data for this study have been obtained from previously published data sets (Caruso et al. 1987; Pezzino 2014). The data about isopods collected for our analysis comprised 72 species, 50 habitats and 17 islands of Sicily's archipelago (Tables II and III). Figure 1 shows the geographical location of the islands considered in this study. The distribution of each species per habitat (following the Corine biotopes classification) is reported in Supplementary Table SI). The main ecological features of each species are reported in Table IV.

Data analysis

Diversity analyses were partially carried out by employing EstimateS software (Colwell 2006), while we utilised SAS University Edition for the other statistical analyses.

Before analysing the data with regressions we checked whether they were normally distributed, with a W/S test for normality, and each of the three variables (area = A; species = S; habitat = H) showed a normal distribution ($Q_{A(n=17)} = 4.11$; $Q_{S(n=17)} = 3.59$; $Q_{H(n=17)} = 3.78$).

We conducted a multiple regression analysis (MRA) to test whether there was any relationship between area and habitat as predictor variables of species richness, considered as a criterion variable. Thus we tested the hypothesis that species richness on islands was correlated with a combination of the extension of the area and the number of the available habitats.

After constructing a linear equation containing all these variables, the multiple regression procedures estimated a linear equation of the form $y = \beta 0 + \beta 1x1 + \beta 2x2 + \varepsilon$, where y is species richness, x1 is logA, x2 is logH and ε is the error due to other unobserved random variables.

We observe that in this equation, the regression coefficients βi ($i = 1,2$) represent the independent contributions of each independent variable to the prediction of the dependent variable. In other words, variable x1 is correlated with the y variable, after controlling for all the other independent variables. This type of correlation is also referred to as a partial correlation.

Thus, we tested the hypothesis that species richness on islands was correlated to a combination of the extension of the area and the number of the available habitats.

We tested the assumption of homogeneity of variance using the residuals of the model (analysis of variance, ANOVA).

We then estimated the variance inflation factor (O'Brien 2007) of the multiple regression analysis to check for multicollinearity between A and H.

To account for multicollinearity and better infer the relationships, we dropped one variable (H) from our analysis; thus, we carried out simple regressions between A and S, and between A and H. A relation between H and S was not tested with simple regression because they showed collinearity and are affected by spurious correlation (both being influenced by A).

We calculated Pearson's r correlation coefficients, linear regression equations, t-test and its significance

Table I. Habitat distribution per island (Corine biotopes classification codes and names).

Corine biotopes	Habitat	Lipari	Vulcano	Salina	Stromboli	Panarea	Filicudi	Alicudi	Ustica	Favignana	Marettimo	Levanzo	Lampedusa	Linosa	Pantelleria	Malta	Gozo	Comino
15.1	Salt pioneer swards			X														
15,725	Sicilian halo-nitrophilous scrubs												X					
16.1	Sand beaches	X	X	X	X	X	X	X		X			X	X				
18.22	Mediterranean cliff communities	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
18.3	Vegetated cliffs of saline lakes														X			
21	Lagoons														X			
22.1	Fresh water			X											X			
31.8A	Tyrrhenian sub-Mediterranean deciduous thickets	X	X	X	X	X	X	X					X					
31,844	Tyrrhenian broom fields				X													
32	Sclerophyllous scrub															X	X	X
32.13	Juniper matorral														X			
32,211	Oleo-lentisc brush								X	X		X		X	X			
32,212	Thermo-Mediterranean heath-garrigues										X							
32,215	Calicotome brush														X			
32.22	Tree-spurge formations			X	X	X	X	X	X	X	X			X				
32.23	Diss-dominated garrigues										X							
32.24	Palmetto brush	X																
32.25	Pre-desert scrub									X	X	X	X	X	X			
32.26	Thermo-Mediterranean broom fields (retamares)		X	X	X			X							X			
32.3	Meso-Mediterranean silicicolous maquis	X	X	X	X	X	X	X										
32.4	Western meso-Mediterranean calcicolous garrigues									X	X	X	X	X	X			
34.5	Mediterranean xeric grasslands	X	X		X	X			X				X	X	X			
34.6	Mediterranean tall-grass steppes	X		X					X	X	X	X	X	X	X			
34.81	Mediterranean subnitrophilous grass communities		X		X		X	X	X	X	X	X	X	X	X			
41.9	Chesnut woods			X														
42	Coniferous woodland															X		
42.82	Mesogean pine forests														X			
42.84	Aleppo pine forests										X				X			
43	Mixed woodland															X		

(*Continued*)

Table I. (Continued).

Corine biotopes	Habitat	Lipari	Vulcano	Salina	Stromboli	Panarea	Filicudi	Alicudi	Ustica	Favignana	Marettimo	Levanzo	Lampedusa	Linosa	Pantelleria	Malta	Gozo	Comino
45.31A	Southern Italian holm-oak forests	X	X		X						X				X			
53.1	Reed beds												X					
61.3B	Central Mediterranean screes										X							
62.14	Southern Italian calcareous cliffs									X	X							
65	Caves															X	X	
66.2	Etna summital communities	X			X													
66.3	Barren lava fields													X	X			
66.4	Volcanic ash and lapilli fields		X		X									X				
82	Crops															X	X	
82.2	Field margin cropland															X	X	
82.3	Extensive cultivation	X	X	X		X	X		X	X		X	X	X	X	X	X	
83.11	Olive groves								X	X					X			
83.15	Fruit orchards								X	X								
83.21	Vineyards	X		X											X	X		
83.31	Conifer plantations		X	X		X			X	X	X	X	X	X	X			
83,324	Locust tree plantations	X		X														
85.1	Large parks									X		X	X					
86	Towns, villages, industrial sites																X	
86.1	Towns	X	X	X	X	X	X	X	X	X	X		X	X	X			
86.3	Active industrial sites								X	X			X	X	X			
86.41	Quarries	X								X			X		X		X	

Table II. Variables analysed for each island of the Sicilian archipelago (V = volcanic; N = non-volcanic).

Island (I)	Linear distance from Sicily (D, km)	Area (A, km^2)	Isopoda species richness (S)	Habitat number (H)	Origin (O)
Stromboli	55.59	12.2	8	13	V
Panarea	41.85	3.34	16	9	V
Salina	38.6	26.4	13	15	V
Filicudi	45.96	9.49	9	8	V
Alicudi	51.45	5	9	8	V
Lipari	28.07	37.6	20	14	V
Vulcano	21.06	20.87	7	12	V
Ustica	53.06	8.65	24	12	V
Levanzo	11.85	5.6	19	9	N
Marettimo	33.36	12.3	31	14	N
Favignana	7	19.8	29	17	N
Pantelleria	85	83	28	24	V
Linosa	160	5.43	14	15	V
Lampedusa	206.53	20	19	16	N
Gozo	94	67.1	20	19	N
Comino	95	2.8	11	5	N
Malta	96	245.7	41	26	N

levels, and determination coefficients (R^2). As in the multiple regression, we tested with ANOVA the assumption of the homogeneity of variance in analysing the residuals.

We computed Jaccard's index of similarity (Chao et al. 2005) for H and S, and we carried out a simple regression analysis to check for a correlation between the diversity of habitat and species among islands.

We built Coleman's rarefaction curves (Coleman et al. 1982) to compare the differences observed in the regression analysis between species and the habitat richness of volcanic and non-volcanic islands.

Finally, we calculated the Marczewski–Steinhaus metric of diversity to check whether there was any relation between β-diversity and the distance of each island from the centre of dispersion (Sicily island).

Results

The multiple regression analysis (Supplementary Table SII) shows that 31% of species richness variation around its mean is explained by a combination of A and H (r = 0.62), but that neither variable is statistically significant ($t_A = -0.17$, $P = 0.87$; $t_H = 1.68$, $P = 0.12$) in a multiple regression against S. We then tested the assumption of homogeneity of variance using the residuals of the model (Supplementary Figure S1). The ANOVA test confirmed this assumption ($F_{(14,2)} = 4.51$ $P < 0.05$).

The variance inflation factor, employed to check for multicollinearity between A and H (VIF = 3.83), shows the presence of a correlation between the two predictor variables (Supplementary Table SII).

The species richness and area of Sicily archipelago islands (species-area curve, SAC) are significantly correlated (Pearson's r = 0.52, $t\text{-test}_{(n=32)} = 3.44$, $P < 0.01$; Figure 2 and Table V). This relation is stronger in non-volcanic ($R^2 = 0.53$) than in volcanic islands ($R^2 = 0.12$). Residual analysis (variance) shows no specific trend ($F_{(16,16)} = 5.53$, $P < 0.05$), so the assumption of constant variance and zero mean in the error terms has been met. Moreover, when rescaled to a log-log relation, the equation $S = cA^z$ returned values of c = 8.91 and z = 0.22.

Habitat richness and area extension of Sicily archipelago islands (habitat-area curve, HAC) are strongly correlated (Pearson's r = 0.86, $t\text{-test}_{(n=32)} = 7.02$, $P < 0.01$; Figure 3 and Table VI). This relation is stronger in non-volcanic ($R^2 = 0.85$) than in volcanic islands ($R^2 = 0.60$). Residual analysis (variance) shows no specific trend ($F_{(16,16)} = 42.49$, $P < 0.001$), so the assumption of constant variance and zero mean in the error terms has been met.

A scatter plot of β-diversity between species and habitats, calculated with Jaccard indexes of similarities (Figure 4 and Table VII), shows a positive relationship with $R^2 = 0.25$.

Coleman's rarefaction curves for species and habitat richness show that non-volcanic islands are always above (richer than) volcanic ones (Figure 5(a) and (b)).

Although we expected to find a positive correlation between Marczewski-Steinhaus β-diversity and the distance of each island from Sicily, the scatter plot (Figure 6) shows no trend ($R^2 = 0.01$) and demonstrates that there is no relation between the distance from the dispersion centre (Sicily) and the β-diversity of species found on satellite islands.

Discussion and conclusion

Results from multiple regression analysis show that species richness is not strongly influenced by a combined effect of area and habitat. However, between area and habitat there is a significant correlation, which was evidenced by the degree of their collinearity in the multiple regression.

To account for multicollinearity and better infer the relationships we dropped one variable (H) from our analysis; thus, we carried out simple regressions between A and S, and then between A and H. A relation between H and S was not tested with simple regression because they showed collinearity and are affected by spurious correlation (both depending on A).

Table III. Incidence data for species distribution on each island of the Sicilian archipelago.

Species/island	Lipari	Vulcano	Salina	Stromboli	Panarea	Filicudi	Alicudi	Ustica	Favignana	Marettimo	Levanzo	Lampedusa	Linosa	Pantelleria	Malta	Gozo	Comino	Total
Acaeroplastes melanurus						X		X	X	X	X	X		X				**7**
Agabiformius lentus	X								X	X	X	X		X	X			**7**
Agabiformius obtusus				X	X			X	X	X		X	X	X	X			**9**
Anaphiloscia sicula								X			X			X	X	X		**5**
Armadillidium aelleni															X	X		**2**
Armadillidium badium	X							X	X		X				X	X	X	**7**
Armadillidium decorum	X							X	X	X	X							**5**
Armadillidium granulatum	X	X	X	X	X	X	X		X	X	X	X		X	X	X	X	**15**
Armadillidium nasatum	X	X	X		X	X	X											**6**
Armadillidium pelagicum								X				X	X	X				**4**
Armadillidium schmalfussi															X	X	X	**3**
Armadillidium vulgare	X	X	X	X	X	X							X		X			**8**
Armadillo officinalis					X			X	X	X	X	X		X	X			**8**
Armadilloniscus candidus								X		X					X			**3**
Armadilloniscus ellipticus						X												**1**
Bathytropa ruffoi										X								**1**
Bathytropa schembrii															X			**1**
Buchnerillo litoralis									X						X			**2**
Chaetophiloscia cellaria	X		X		X										X		X	**5**
Chaetophiloscia elongata	X		X		X				X	X				X	X	X	X	**9**
Ctenoscia dorsalis					X				X	X	X	X	X	X	X			**8**
Halophiloscia couchii			X				X	X	X	X		X	X	X	X	X		**10**
Halophiloscia hirsuta								X	X	X		X	X	X	X	X		**8**
Haplophthalmus avolensis															X			**1**
Hiblaeoniscus vallettai															X	X		**2**
Leptotrichus naupliensis	X														X	X	X	**4**
Leptotrichus panzerii	X	X	X	X	X			X	X	X	X	X	X	X	X	X	X	**15**
Ligia italica					X	X		X	X		X	X	X	X	X	X	X	**11**
Mica tardus									X									**1**
Miktoniscus melitensis															X			**1**
Philoscia affinis								X	X	X	X				X			**5**
Platyarthrus aiasensis	X		X		X	X		X	X	X	X	X	X	X	X	X	X	**14**
Platyarthrus briani	X				X													**2**
Platyarthrus caudatus	X			X			X	X	X	X	X				X	X		**9**
Platyarthrus costulatus	X			X	X	X	X			X				X				**7**
Platyarthrus esterelanus										X					X			**2**
Platyarthrus lerinensis										X					X	X		**3**
Plathyartrus schöbli codinai									X									**1**
Platyarthrus schöbli intermedius	X		X												X			**3**
Plathyartrus schöbli schöbli														X				**1**
Porcellio albicornis	X																	**1**
Porcellio hyblaeus																X		**1**
Porcellio imbutus									X	X	X							**3**
Porcellio laevis	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	**16**
Porcellio lamellatus									X	X	X	X	X	X	X	X		**8**

(*Continued*)

Table III. (Continued).

Species/island	Lipari	Vulcano	Salina	Stromboli	Panarea	Filicudi	Alicudi	Ustica	Favignana	Marettimo	Levanzo	Lampedusa	Linosa	Pantelleria	Malta	Gozo	Comino	Total
Porcellio obsoletus									X							X		**2**
Porcellio parvus									X									**1**
Porcellio siculoccidentalis										X	X							**2**
Porcellio spatulatus										X								**1**
Porcellio tripolitanus pelagicus												X						**1**
Porcellionides myrmecophilus	X								X	X					X	X	X	**6**
Porcellionides pruinosus	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	**16**
Porcellionides sexfasciatus		X			X				X	X	X							**5**
Proporcellio vulcanius														X	X	X		**3**
Spelaeoniscus cfr. *costai*								X										**1**
Spelaeoniscus cfr. *lagrecai*										X								**1**
Spelaeoniscus coiffaiti														X				**1**
Spelaeoniscus costai								X										**1**
Spelaeoniscus lagrecai										X								**1**
Spelaeoniscus vandeli														X				**1**
Spelaeoniscus sp.														X				**1**
Stenoniscus carinatus								X	X	X		X	X	X	X			**7**
Stenoniscus pleonalis														X				**1**
Stenophiloscia glarearum								X							X			**2**
Stenophiloscia zosterae			X					X				X		X				**4**
Trichoniscus halophilus								X				X		X	X			**4**
Trichoniscus matulicii															X			**1**
Trichoniscus pusillus s. l.							X											**1**
Trichoniscus pymaeus			X					X							X			**3**
Trichorina paolae															X			**1**
Trichorhina sicula										X								**1**
Tylos europaeus												X				X		**2**
Tylos ponticus	X						X		X				X	X				**5**
Total	**20**	**7**	**13**	**8**	**16**	**9**	**9**	**24**	**29**	**31**	**19**	**19**	**14**	**28**	**41**	**23**	**12**	

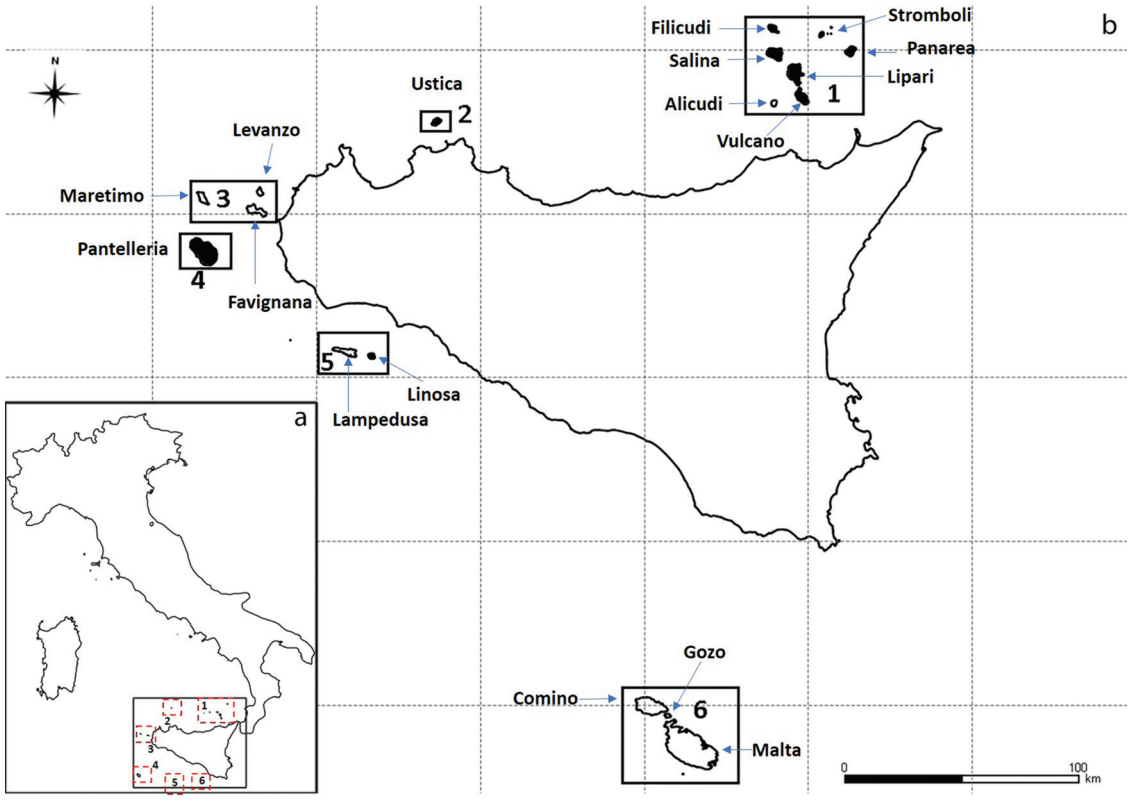

Figure 1. Study area. 1: Vulcano, Lipari, Alicudi, Filicudi, Salina, Panarea, Stromboli; 2: Ustica; 3: Favignana, Marettimo, Levanzo; 4: Pantelleria; 5: Lampedusa, Linosa; 6: Malta, Comino, Gozo. Volcanic islands are coloured black; not-volcanic ones are white. The locations of the islands in 4 and 5 do not correspond to reality in order to facilitate the visualisation.

In the analysed islands, 27% of species richness variation is explained by the area. Moreover, we see a strong influence of the area on habitat richness (74% of H variation is due to the area of the island). Therefore, although there is no directly coupled effect of A and H on S, area extension influences both isopods and their habitat richness. We can speculate that because the correlation between A and H is more significant than that between A and S, the species-area relationship is mainly due to an indirect effect, which is mediated by the stronger relationship between the amount of area and the number of available habitats present in that area. In other words, we find a positive relationship between area and species probably because the number of habitats available for species rises according to the increase of the areal extension.

We suppose that a relation between the diversity of habitat and species among islands could have been a consequence of the correlation patterns observed. Hence we plotted the β-diversity (Jaccard's index of similarity) of H against that of S and we carried out a simple regression analysis (Figure 4 and Table VI). We show that this relationship is positive and quite strong ($r = 0.49$; ANOVA $F = 33.76$, $P < 0.01$), which means that the diversity of habitats among the analysed islands explains 24% of the variation of richness.

Moreover, we show that rarefying at the minimum common number of islands ($n = 5$), both species and habitat richness of non-volcanic islands are higher than those of volcanic ones. This may be due to the geology of the soil because it is well known that most *Oniscidea* species prefer calcified soils (Vandel 1960). Thus, on volcanic islands, the number of species per unit of area is almost always less than that on non-volcanic calcareous islands (e.g. Lampedusa, Marettimo, Favignana, Levanzo).

Considering habitat and species' ecology and distribution (Tables I, III and IV), Sicily, because of its position in the middle of the Mediterranean, is a faunistic hot spot. The island can be considered an appendage of both North Africa and the Italian peninsula. La Greca (1957) claimed that the most interesting aspect of the Sicilian isopod populations is that their origin is not so much North African but Tyrrhenian. However, during the Messinian, the closure of communications between the Atlantic and the

Table IV. Main ecological features of the isopod species analysed in this study.

Species	Main ecological features
Acaeroplastes melanurus	A species that does not stray far from the sea. It is well represented even though most of the findings refer to lowland areas. However, in some cases, it was collected even above 1000 m altitude.
Agabiformius lentus	This species lives mainly under stones in sandy soils; it often shares the same environment with *Leptotrichus*. It is a moderately xerophilous species with anthropophilous tendencies; we find it often linked to human activities. In Sicily, it was also found in karst caves.
Agabiformius obtusus	This species seems to have more hygrophilous habits than *A. lentus*; in fact, it has always been found near the coast under the stones of flatlands.
Anaphiloscia sicula	Endogenous species found in several stations near the sea and under well-buried stones.
Armadillidium aelleni	Troglophile species (perhaps troglobius); it has never been found outside the caves.
Armadillidium badium	Species of meadows, very abundant. It has a wide ecological tolerance, so much so that it is possible to observe it from the shores of the sea up to 1000 m altitude; it prefers open and non-wooded areas.
Armadillidium decorum	This species is widely present in Sicily and on the islands; it is found both in the plains and in the mountains up to 1500 m above sea level, often in beech and oak forests.
Armadillidium granulatum	Species littoral, but not halophile; it is considered characteristic of the area with dominant vegetation of *Crythmum maritimum*. It is also found in the hinterland.
Armadillidium nasatum	It is a species with a wide ecological tolerance; in fact, it is also found in caves over the plains and in the mountains even above 1000 m of altitude.
Armadillidium pelagicum	It is a fairly xerophilous species that is found under stones until the end of spring.
Armadillidium schmalfussi	Endemic species present on every island of the Maltese Archipelago where it lives in all biotopes, caves excluded. It is perhaps the most abundant and most ubiquitous *Armadillidium* of these islands.
Armadillidium vulgare	Anthropophile species with a very wide distribution and an extraordinary ecological value. In fact, it is found from sea level up to rather high altitudes. In Sicily it has been observed above an altitude of 1000 m.
Armadillo officinalis	Xerophilous species very common in Sicily and also present on the islands. It is often found in dry and rocky biotopes and with very sunny exposures, so much so that it can often be active even at high temperatures. Its thermal optimum would be 21.9°C. In France, this species only populates regions of low altitude. But in warmer countries, this species is found not only on the plains but also in the mountain regions. It reaches 1200 m aboe sea level in the south of Spain (Alpujarra) and 1800 m in Lebanon. It has nocturnal habits; during the day, it stays under the stones, but at night it shows great activity. It can emit sounds that can be heard by the human ear.
Armadilloniscus candidus	Halophilous species found in the immediate proximity of the coast under well-buried stones and under organic residues.
Armadilloniscus ellipticus	Halophilous species. In Pantelleria around 100 specimens have been collected, living between the lentisk litter and under large stones, along the shores of the lake Specchio di Venere, which is about 1 km from the sea.
Bathytropa ruffoi	Endogenous species.
Bathytropa schembrii	Endogenous species.
Buchnerillo litoralis	A halophile species living in the immediate vicinity of the sea under piles of beached posidonias or under large rocks. Presumably, in Sicily and on the islands, it is much more widespread, and its apparent localisation is probably due to a lack of observations because they are very small animals that easily escape from sight.
Chaetophiloscia cellaria	Troglophile species, very frequent in limestone caves, volcanic caves and even tunnels. It is also found under very well-buried stones and often also in litter.
Chaetophiloscia elongata	It is a very well-represented species both in Sicily and on small islands. It prefers lowland areas with a high humidity and never gets far from the sea, marshes and rivers; it is absent in mountain areas although in Sicily it has been found up to 1000 m and, although rarely, also in a beech forest.
Ctenoscia dorsalis	It is a lowland humic species, which is often found in litter and in contact with the ground under well-buried stones.
Halophiloscia couchii	A strict halophile species that is easily found along the coasts under stones and organic residues.
Halophiloscia hirsuta	Halophilous species that lives a little farther from the sea, along the coast in the stations affected by *Crithmo-Lemonietea* vegetation or the *Ammophiletea*.
Haplophthalmus avolensis	This species can be considered troglophilous or endogenous.
Hiblaeoniscus vallettai	Endogenous species living under well-buried stones a short distance (50 m) from the sea.
Leptotrichus naupliensis	Moderately xerophilous species. It lives under rocks or in sandy soils where it is rapidly buried – without, however, digging stable tunnels.
Leptotrichus panzerii	Moderately xerophilous species. It lives under rocks or in sandy soils where it is rapidly buried – without, however, digging stable tunnels. Frequently it is found with *Leptotrichus naupliensis*.
Ligia italica	This species is strictly alophilous and associated with the sea. It is a species of the sublittoral along all the coasts of Sicily and of the small islands.
Mica tardus	It is a typical species of open and humid places; lives in preference on loose land.
Miktoniscus melitensis	The species prefers very humid places located in the immediate vicinity of the sea.
Philoscia affinis	A frequently encountered species, it is found in biotopes with a high percentage of humidity: very humid meadows, banks of rivers, around lakes, and in the litter of woods, where it reaches a maximum altitude of 1200 m above sea level.

(*Continued*)

Table IV. (Continued).

Species	Main ecological features
Platyarthrus aiasensis	Myrmecophilous species. Parthenogenetic in some geographical areas, bisexual in others.
Platyarthrus briani	This species has always been found with ants of different species, so it can be considered a myrmecophile, like all species of the genus.
Platyarthrus caudatus	Myrmecophilous species very common in Sicily and on the islands.
Platyarthrus costulatus	A species that only occasionally lives with ants; in fact, in most cases it was collected without. It behaves like an endogenous species, being frequently found under large stones or between roots of various plant species.
Platyarthrus esterelanus	Myrmecophilous species that does not move far from the sea. Very common in the French Mediterranean region, it is now also known for Sicily and Marettimo.
Platyarthrus lerinensis	The species can be considered endogenous rather than myrmecophile.
Plathyartrus schöbli codinai	Myrmecophilous species.
Platyarthrus schöbli intermedius	Myrmecophilous species.
Plathyartrus schöbli schöbli	Myrmecophilous species.
Porcellio albicornis	Species often found with ants in open and uncultivated areas, ferulets, stony plains; it prefers calcareous substrates.
Porcellio hyblaeus	It is commonly found in every biotope except for caves.
Porcellio imbutus	In Sicily it is commonly found in every biotope, with the exception of the caves. However, the species seems to prefer forest biotopes, where it was collected at up to 1500 m altitude in the beech litter.
Porcellio laevis	Anthropophilous species, with a wide ecological tolerance. It has colonised all the lands where man is present; it is possible to observe it in garden debris, in cellars, near sheepfolds and on farms, near dung, etc. It prefers stone, formerly cultivated areas and open lands in general.
Porcellio lamellatus	This species is classically referred to as halophilous, although it lives on the shoreline a bit more inland from where *Tylos*, *Ligia* and some species of *Halophiloscia* live. Despite this, some populations have been observed in two locations on the northern slopes of Etna, at about 700 m above sea level and 20 or more km from the sea.
Porcellio obsoletus	Species of gardens and meadows.
Porcellio parvus	Species of gardens and meadows.
Porcellio siculoccidentalis	It is commonly found in every biotope, with the exception of caves; very common in meadows.
Porcellio spatulatus	The Marettimo populations were observed in locations near the coast, in the fissures of calcareous rock where organic debris accumulates. In Sicily it was found also in a location far from the coast.
Porcellio tripolitanus pelagicus	The ecology of this species is still unknown.
Porcellionides myrmecophilus	Myrmecophilous species, widely present in Sicily and on the circumsicilian islands; it always lives with the granivorous ants of the genus *Messor*.
Porcellionides pruinosus	Very common species related to man and human activities: it is often found in homes, and can be defined as anthropophilous.
Porcellionides sexfasciatus	Species of lowlands that seldom strays far from the coast. It is often found in anthropised environments, e.g. gardens, vegetable gardens and cultivated areas in general.
Proporcellio vulcanicus	Thermophilous species collected near fumaroles or secondary volcanic eruptions (Terme di Sciacca).
Spelaeoniscus cfr. *costai*	Endogenous species observed under well-buried stones not very far from the sea. The species until now has been considered endemic.
Spelaeoniscus cfr. *lagrecai*	Endogenous species.
Spelaeoniscus coiffaiti	Representatives of the genus *Spelaeoniscus* are all mostly endogenous species with low vagility.
Spelaeoniscus costai	Endemic to the island of Ustica.
Spelaeoniscus lagrecai	Endogenous species.
Spelaeoniscus vandeli	Humicolous and endogenous species collected near the sea.
Stenoniscus carinatus	Halophilous species. In Pantelleria around 100 specimens have been collected, living in lentisk litter and under large stones, along the shores of the lake Specchio di Venere, which is about 1 km from the sea.
Stenoniscus pleonalis	Halophilous species living among the old seagrasses on the coast and beneath the rocks in the immediate vicinity of the sea.
Stenophiloscia glarearum	Halophilous species that is found in the immediate vicinity of the sea under the rocks and under organic materials of various kinds.
Stenophiloscia zosterae	This species is largely confined to coastal shingle.
Trichoniscus halophilus	Halophilous species found in the immediate vicinity of the sea and associated with *Halophiloscia*, *Buchnerillo and Stenoniscus*.
Trichoniscus matulicii	In Sicily and Malta this species seems to live only in caves and can, therefore, be considered either troglophilous or behaves as such in southern Italy.

(*Continued*)

Table IV. (Continued).

Species	Main ecological features
Trichoniscus pusillus s. l.	A species sensitive to desiccation and therefore very specific with regard to humidity conditions. It is only found in environments saturated with humidity: banks of rivers and lakes, moss in the springs and very humid litter. In Sicily this species is found to be abundant both in caves and outside them and is present from sea level up to 1500 m altitude (Piano Battaglia, Palermo).
Trichoniscus pygmaeus	A humic species that, especially along the southern margin of its range, lives essentially as an endogenous species and is found under large, well-buried stones.
Trichorina paolae	Species probably troglobious.
Trichorhina sicula	This species is found under large well-buried stones and can, therefore, be considered an endogenous species; it is so sensitive to desiccation that a few minutes of exposure to the open air can kill it.
Tylos europaeus	Typically halophilous species that is found in the immediate vicinity of the sea, under stones or in the sand where it digs tunnels.
Tylos ponticus	Halophilous species that is found in the immediate vicinity of the sea, under stones or in the sand where it digs tunnels.

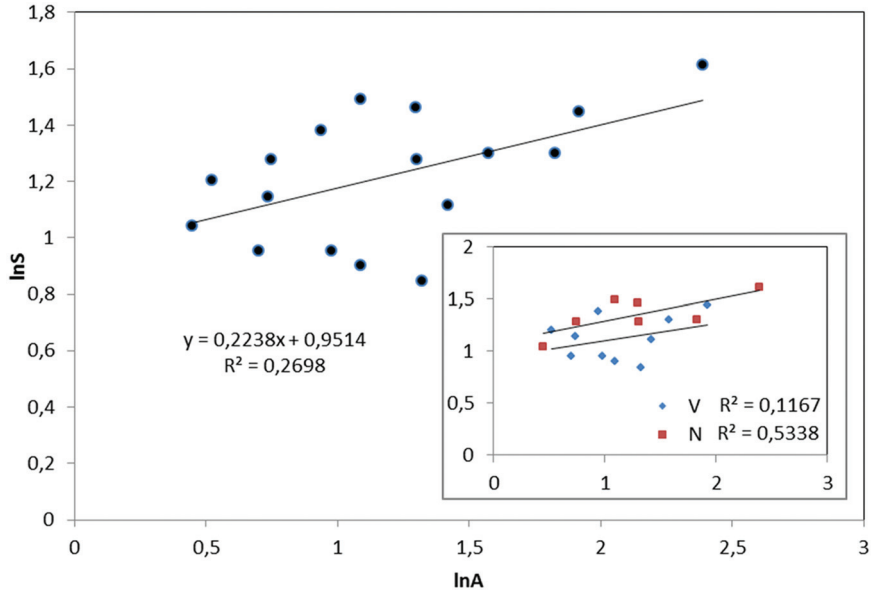

Figure 2. Species-area curve (SAC) in log-log transformation. Linear regression equation and line are shown. R^2 is the coefficient of determination. The inset presents a regression analysis for data grouped according to volcanic (V) or non-volcanic (N) origin.

Table V. Analysis of variance and residuals of the species-area curve (see also Figure 2). SD: standard deviation; VIF: variance inflation factor.

Parameter	Est. value	SD	t student	Prob (> |t|)
b0	0.95	0.12	7.71	1.35E-06
b1	0.22	0.09	2.35	0.03
Residual SD	0.20			y = b0 + b1.x1
R^2	0.27			
F	5.54		**Pearson's r**	0.52
Prob (> F)	0.03		**t-test (r)** P = 0.01, n = 32	3.44

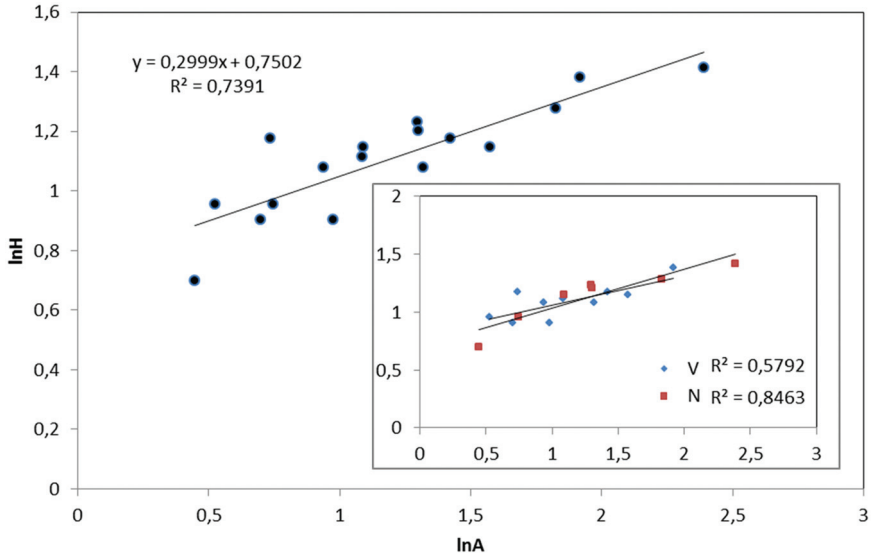

Figure 3. Habitat-area curve (HAC) in log-log transformation. Linear regression equation and line are shown. R^2 is the coefficient of determination. The inset presents a regression analysis for data grouped according to volcanic (V) or non-volcanic (N) origin.

Table VI. Analysis of variance and residuals of the Habitat-Area curve (see also Figure 3). SD: standard deviation; VIF: variance inflation factor.

Parameter	Est. value	SD	t student	Prob (> |t|)
b0	0.75	0.06	12.57	2.29E-09
b1	0.30	0.05	6.52	9.71E-06
Residual SD	0.10			y = b0 + b1.x1
R^2	0.74			
F	42.49		**Pearson's r**	0.86
Prob (> F)	9.71E-06		**t-test (r)** P = 0.01, n = 32	7.02

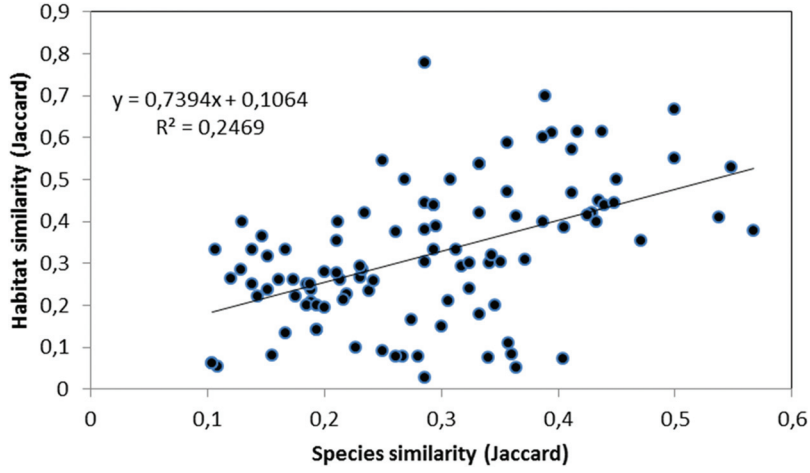

Figure 4. Scatter plot of β-diversity between species and habitats. Values are Jaccard indexes of similarity. R^2 is the coefficient of determination (linear regression equation and line are shown).

Table VII. Regression analysis of β-diversity between species and habitats (see also Figure 4). SD: standard deviation.

Parameter	Est. value	SD	t student	Prob (> |t|)
b0	0.106397	0.039225	2.71246	0.007828
b1	0.739413	0.127247	5.810838	6.99E-08
Residual SD	0.143244			y = b0 + b1.x1
R^2	0.246888		**Pearson's r**	0.496878
F	33.76583		**Prob (> F)**	6.99E-08

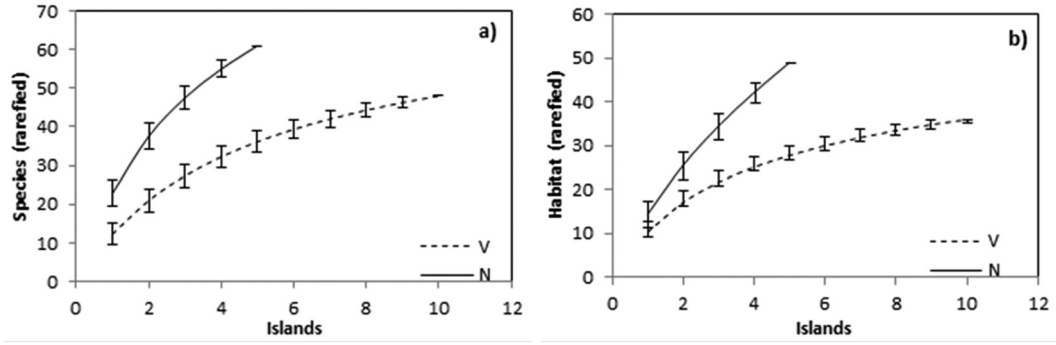

Figure 5. Coleman's rarefaction curves of (a) species and (b) habitat diversity for islands of volcanic (V) and non-volcanic (N) origin.

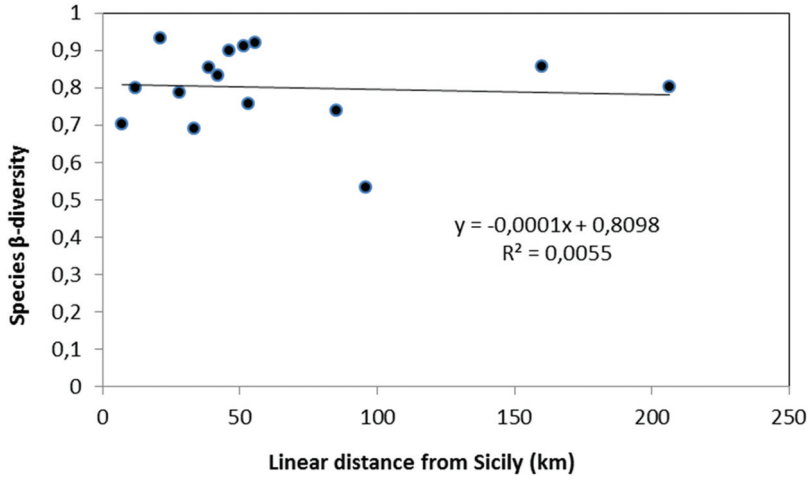

Figure 6. Scatter plot of β-diversity and distance between Sicily and each island. β-diversity values are from the Marczewski–Steinhaus metric. R^2 is the coefficient of determination (linear regression equation and line are shown).

Mediterranean Sea, and the consequent desiccation, would have made territorial connections possible also between North Africa and Sicily, favouring faunal and vegetational exchanges (Giachino et al. 2011).

The probable subsequent division of the territory into islands, formed between North Africa and Sicily, led to numerous speciation events, some of which ended with the evolution of independent species. Then, the colonisation of Sicily gave rise to a subsequent adaptive radiation as a response to the new environmental situations that induced other speciations and therefore the origin of other species (Cazzolla Gatti 2011; Pezzino 2014).

For instance, it should be noted that the species of the family *Spelaeoniscidae* are characterised by little vagility and therefore they easily tend to isolate and differentiate (Lombardo et al. 2006); this is demonstrated by the high number of endemic species and by the fact that almost all species are very localised (Pezzino 2014; Caruso et al. 2017).

The genus *Spelaeoniscus* and the genus *Hybleoniscus* currently have a Mediterranean-western distribution, being present in Morocco, Algeria, Northern Sahara, Balearic Islands, Southern Spain, Sicily and the Circumeric islands. This distribution confirms a remarkable old phylogeny of the *Spelaeoniscidae* family that probably originated in the territory of Tirrenide during the Tertiary following the complex geological events of these lands. From the primitive lineage, some populations would have been isolated and differentiated into the many species and genera that we found in the analysed data sets.

Considering the current distribution and presence of these species in various geographical areas (Vandel 1960), we can probably suppose that *Spelaeoniscus* originated in North Africa; the presence in this African region of *Hibleoniscus*, which currently seems to be confined to the Ibleo-Maltese territory, cannot be excluded. On the other hand, it is known that Sicily up to the Mindelian was still divided into two territories of which the southern Iblei were perhaps connected with North Africa (La Greca 1957). The current distribution of the genera *Spelaeoniscus* and *Hiblaeoniscus* that we consider in this study (emerging from the analysed data sets) seems to be the result of a migration to the north, towards the less arid regions (Vandel 1960).

Moreover, the presence of *Trichoniscus matulicii*, a species with trans-Adriatic distribution, suggests a dispersion of this species in Sicily, which occurred during one of the quaternary Calabrian-Sicilian connections.

We showed (Table III) that between Sicily and the Aeolian Archipelago there are several common species. This could suggest possible territorial connections between some of the Aeolian Islands and Sicily. The Aeolian Islands, which are the product of Pleistocene volcanic eruptions, may be considered an ancient base of non-volcanic nature that probably emerged before and during the beginning of the eruptive period (Caruso 1973). It is, therefore, possible that before the formation of the volcanic systems, between the Aeolian Archipelago and Sicily some connections existed and some strips of land remained for a long time, allowing a certain passage of fauna between the two territories. This does not exclude that a high number of species have also reached the neighbouring volcanic islands transported by men and/or floating rafts.

The comparison of Sicilian species with those of the Egadi Archipelago (Table III) highlights a greater affinity between the main island and Favignana and Marettimo. The high number of common halophile species between Sicily and the islands of the Archipelago can be easily explained, taking into account the ease with which these species can spread on the coasts of close islands without any specific acclimation requirement (Table IV).

The presence of *Porcellio siculoccidentalis* on the western side of Sicily and on the other small islands shows a colonisation and/or a passage of this species during periods in which Favignana had contact with the major island. The presence of this species on Marettimo is more difficult to explain except for a passive colonisation (anthropogenic factors). Marettimo also shows a similarity to Sicily (Table III) in the presence of both *Platyarthrus costulatus* and *Spelaeoniscus lagrecai*, which are absent on the other two islands. The presence of *Trichorhina sicula* on Marettimo leads us to hypothesise a possible connection with Sicily, bearing in mind that this species is particularly delicate and extremely sensitive to desiccation (Table IV).

Almost all the Ustica species are present in Sicily (Table III); the only two that characterise the fauna of this small island are *Spelaeoniscus costai*, a probable neoendemism of this island, and *Armadillidium pelagicum*, whose presence on this island is difficult to explain. The species is also known from Tunisia, Pantelleria and the Pelagie Islands. Considering that Ustica is a small, entirely volcanic island that is very far from the Sicilian coasts (Table II), we can only argue that the *Spelaeoniscus costai* population, at least in the light of current knowledge, is of invasive origin; a small population of *Spelaeoniscus* could have reached the island and, subsequently, differentiated here; in fact, this species has a very low vagility and seems to have a rapid speciation capacity (Table IV).

The island of Pantelleria, although it is among the largest of the small Circumsicilian Islands and second only to Malta (Table II), hosts a relatively low number of species. Ninety percent of these species has also been observed in Sicily (Table III). The presence on both islands of *Proporcellio vulcanius* may be explained considering the ecological needs of this thermophilous species (Table IV), which prefers environments still affected by secondary volcanism. It seems to have been widely dispersed by human beings, far from its probable centre of origin (Vandel 1960).

The Pelagie also include a low number of species which are all found in common with Sicily (Table III), except for *Armadillidium pelagicum*, distributed only on Ustica, Pantelleria, Pelagie and Tunisia. The presence of this species also in Tunisia clearly indicates that this island has had recent contact with North Africa.

The islands of the Maltese Archipelago have notable affinities with Sicily (Table III); in fact, most of its species are shared with the major island and this

may confirm the hypothesis (La Greca 1961; Caruso 1982) of an Ibleo-Maltese territory. The presence in both territories of *Miktoniscus melitensis*, *Trichorhina paolae* distributed in Sicily exclusively in the Iblaean territory, and *Haplophthalmus avolensis*, which is very well represented in this area, is relevant. Sicily and the Maltese archipelago are therefore differentiated by their endemisms (Tables III and IV). However, the affinities between this Archipelago and North Africa are unclear and, in any case, it is possible to state, on the basis of our results, that few species have remained on the Archipelago during periods of territorial connection.

In general, the affinities between the isopods of North Africa and Sicily are considered to be not very relevant (La Greca 1961; Caruso 1982; Pezzino 2014). On the basis of the available data it can be argued that Sicily received some isopod species from North Africa (for example *Spelaeoniscidae* spp.); meanwhile it probably constituted a bridge through which thermophilous species (Table IV), pushed by the lowering of the temperature during the glacial periods, reached North Africa, moving in the opposite direction.

In conclusion, we show that particularly close affinities have emerged from the comparison of Sicily and the Maltese Archipelago's isopod species (Table III). With regard to the total population of all the other islands considered in this study, a substantial homogeneity has emerged even if some neo-endemisms are particularly interesting and provide some evidence about the colonisation and the age of the island.

Nevertheless, considering Sicily as the possible centre of dispersion for most of the species found on satellite islands (Caruso et al. 1987), we checked whether there was a correlation between species richness of each island and the distance from Sicily. This correlation was very weak, with $R^2 = 0.0055$ and a slope of −0.01. The absence of an expected positive relationship between β-diversity and the distance of each island from Sicily could be due to anthropogenic influences (such as ballast water; tourism; soil, fertilisers and ornamental plant transportation, etc.; Cazzolla Gatti 2016c) and natural events (such as rafting on wood or floating seeds, island hopping, etc.). These factors could have played important roles in homogenising the diversity among islands, despite the relative distance.

Finally, our results could be considered an integrative analysis with respect to other published data sets, such as those of Sfenthourakis (1996) and Gentile and Argano (2005), who studied the distribution of the same taxa on Aegean and Mediterranean islands. Gentile and Argano (2005), in particular, analysed similarity indexes and showed that small islands of the Mediterranean Sea can be divided into two major groups: eastern and western. Moreover, they reported that islets were characterised by a few common species with large ranges, even if the species–area logarithmic model did not always provide the best fit. Our results, although confirming the previous evidence, added other factors to explain the SAR. In fact, we showed that taking into account habitat and ecological diversity of the isopods, and evaluating them in the framework of geological dynamics, a better interpretation of their biogeography and, in this case, of the species-area relationship is possible, not only invoking the "small island effect", which may just be an artefact depending more on statistical techniques (Burns et al. 2009) than on natural history.

Disclosure statement

No potential conflict of interest was reported by the authors.

Supplemental data

Supplemental data for this article can be accessed here.

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