

On the road of dung: hypothetical dispersal routes of dung beetles in the circum-Sicilian volcanic islands

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Abstract

On the road of dung: hypothetical dispersal routes of dung beetles in the circum-Sicilian volcanic islands.— We analysed dung beetle communities on ten volcanic islands located around Sicily (Italy) to identify the most probable dispersal routes in the colonization of these islands. Assuming two scenarios, we analysed the dung beetle communities through the coefficient of dispersal direction DD_2 . Our results suggest that dispersal fluxes do not strictly follow the 'stepping stone' dynamic. Lipari and Vulcano are the likely core source areas for the north-of-Sicily area. In the Sicily Channel, Linosa appears to have been the main target area with three equivalent fluxes from Tunisia, Sicily, and Malta, while the fauna of Pantelleria resulted from their interchange and proximity to Tunisian fauna. In light of the congruence of our results with the known history of human movements and colonization, we propose a likely human contribution to the genesis of the dung beetle fauna of the circum-Sicilian volcanic islands.

Key words: Dung beetles, Island biogeography, *Thorectes intermedius*, Stepping stone dispersal

Resumen

En el camino del estiércol: rutas de dispersión hipotéticas de los escarabajos coprófagos de las islas volcánicas circumsicilianas.— Se han analizado las comunidades de escarabajos del estiércol que habitan diez islas volcánicas localizadas alrededor de Sicilia (Italia), con el propósito de determinar las posibles rutas de dispersión que se siguieron en la colonización de estas islas. Utilizando dos supuestos diferentes, hemos analizado las comunidades de escarabajos coprófagos mediante el coeficiente de dirección de la dispersión DD_2 . Los resultados obtenidos sugieren que los flujos de dispersión no han seguido estrictamente una dinámica de 'stepping stone' (puntos de paso). Lípari y Vulcano habrían sido las principales fuentes de colonización de las zonas del norte de Sicilia. En el canal de Sicilia, Linosa habría sido la principal zona de destino con tres flujos equivalentes procedentes de Túnez, Sicilia y Malta, mientras que la fauna de Pantelaría se explicaría por la conexión y cercanía de la isla con Túnez. Debido a la fuerte congruencia de nuestros resultados con la historia de los movimientos y colonizaciones humanas en estas zonas, proponemos que probablemente el factor antrópico haya contribuido a la génesis de la fauna de escarabajos del estiércol de las islas volcánicas circumsicilianas.

Palabras clave: Escarabajos coprófagos, Biogeografía insular, *Thorectes intermedius*, Dispersión por puntos de paso

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Introduction

Islands are among the areas of the world that have most aroused the curiosity of naturalists, long attracted by their peculiarities such as geographical isolation, small size and, at least for volcanic islands, recent age (Whittaker & Fernández-Palacios, 2007). Because of the relative simplicity of studying an island (Vitousek, 2002), many studies of these environments have become paradigmatic (MacArthur & Wilson, 1967; Simberloff, 1974). Islands are ideal contexts to conduct a natural historical experiment (Diamond & Robinson, 2010).

In biogeographical terms, we can distinguish two major categories of islands: continental and oceanic. The former are located on the continental shelf and may have been linked to the mainland in the past, while the latter have never been connected to the mainland (Whittaker & Fernández-Palacios, 2007). This distinction has conceptual implications of great importance. Since the beginning of the modern debate 'dispersal versus vicariance' (Croizat et al., 1974; Heads, 2014), the dispersalist approaches have undergone considerable criticism (Morrone & Crisci, 1995 and references cited therein). The non-refutability of dispersalist explanations, defined *ad hoc* (for review: Morrone & Crisci, 1995; Bueno Hernández & Llorente-Bousquets, 2000; Zunino & Zullini, 2004), has shifted focus towards vicariantist arguments. This paradigm shift has consequently led to a lack of interest in respect to oceanic islands due to the non-falsifiability of hypotheses (Cowie & Holland, 2006). However, in recent years, the importance of dispersal as a key mechanism in determining species distribution has been emphasized (De Queiroz, 2005; Cowie & Holland, 2006) and oceanic islands have attracted attention because their biodiversity pattern must necessarily be explained in dispersal terms (Cowie & Holland, 2006). In this context, the value of biodiversity analysis methods should be stressed (Magurran & McGill, 2011), especially regarding the beta diversity that Whittaker (1960, 1972) has defined as "the extent of change in community composition". In recent years, studies concerning the beta diversity have proliferated (Anderson et al., 2011). This interest in the study of beta diversity is linked to a basic question of community ecology —what makes a set of species more or less similar to another in different times and spaces (Vellend, 2010)?.

Several studies on different taxa and scales have addressed the issue of the distribution, composition and species richness of organisms from an eco-biogeographical perspective, aiming to identify the key variables that could explain these patterns (Freestone & Inouye, 2006; Veech & Crist, 2007; Qian, 2009; Bin et al., 2010; Jiménez-Valverde et al., 2010; Vellend, 2010; Baselga et al., 2012; Dexter et al., 2012). These studies have also focused on island environments and multiple studies have analysed the factors controlling the spatial patterns of biodiversity among many taxa (Kadmon & Pulliam, 1993; Legakis & Kyriotakis, 1994; Palmer, 1998; Palmer et al., 1999; Garcia-Barros et al., 2002; Guerrero et al., 2005; Hausdorf & Hennig, 2005;

Dapporto & Cini, 2007; Fattorini, 2009a, 2009b, 2010; Sfenthourakis, 1996; Dennis et al., 2000). Fattorini (2010), for example, investigated the importance of island areas, distance from the continent, inter-island distance and island age of the Aeolian archipelago (southern Italy) in determining patterns of spatial variation in beta diversity for several taxa, including dung beetles. In this research, Fattorini concluded that the dung beetle fauna originated quite recently and that the species were established on the islands by a 'stepping stone' dispersive process: species dispersed from one island to the nearest (MacArthur & Wilson, 1967). However, in an attempt to reconstruct the dispersal patterns of coprophagous fauna, Fattorini (2010) identified conflicting results. Specifically, his analysis of similarity (with Jaccard and Kulczynski 2 indices) produced three different clusters, which cannot provide an unambiguous explanation. Furthermore, these indices are not appropriate for the exploration of dispersal fluxes because they cannot identify the direction of dispersal. Using an expanded database (in terms of areas and dung beetle species) and inspired by Fattorini's (2010) paper, we attempted in this exploratory research to reconstruct the possible dispersal routes of dung beetle fauna in the colonization of circum-Sicilian volcanic islands in order to formulate a *posteriori* hypothesis about the probable mechanisms involved in the conformation of these island assemblages.

Material and methods

Study area

The survey focused on 10 volcanic islands: eight located north of Sicily (Ustica and the Aeolian archipelago: Lipari, Salina, Vulcano, Stromboli, Filicudi, Alicudi, Panarea) and two in the Sicily Channel (Pantelleria and Linosa) (fig. 1).

At no point in the past were these islands connected to continental areas, allowing us to exclude vicariance events. The oldest islands are Linosa and Ustica (about 1,000 Kyr). Their age excludes any involvement in the Messinian salinity crisis, which ended about 5.3 million years ago (Krijgsman et al., 1999). This period had a tremendous impact on the biogeography of the Mediterranean fauna (Sanmartín, 2003; Marra, 2005). The estimate of the most severe sea-level drops over the last 5.3 million years is -120 m (Rohling et al., 2014). The Aeolian archipelago is separated from Sicily by a channel between 1,000 and 2,000 m deep, while the interisland depth varies from 400 to 1,400 m. Only Lipari and Vulcano, divided by water depths < 50 m, were connected to each other but they were always separated from Sicily during glacial periods of sea-level lowering. Ustica is the summit of a large volcanic edifice resting on the seabed at depths of the order of 2,000 m (Ruggieri, 1973; Marani et al., 2004). Pantelleria and Linosa were also isolated during glacial phases (Shackleton et al., 1984).

Although the hypothetical dispersal routes were investigated only for volcanic islands, we also examined

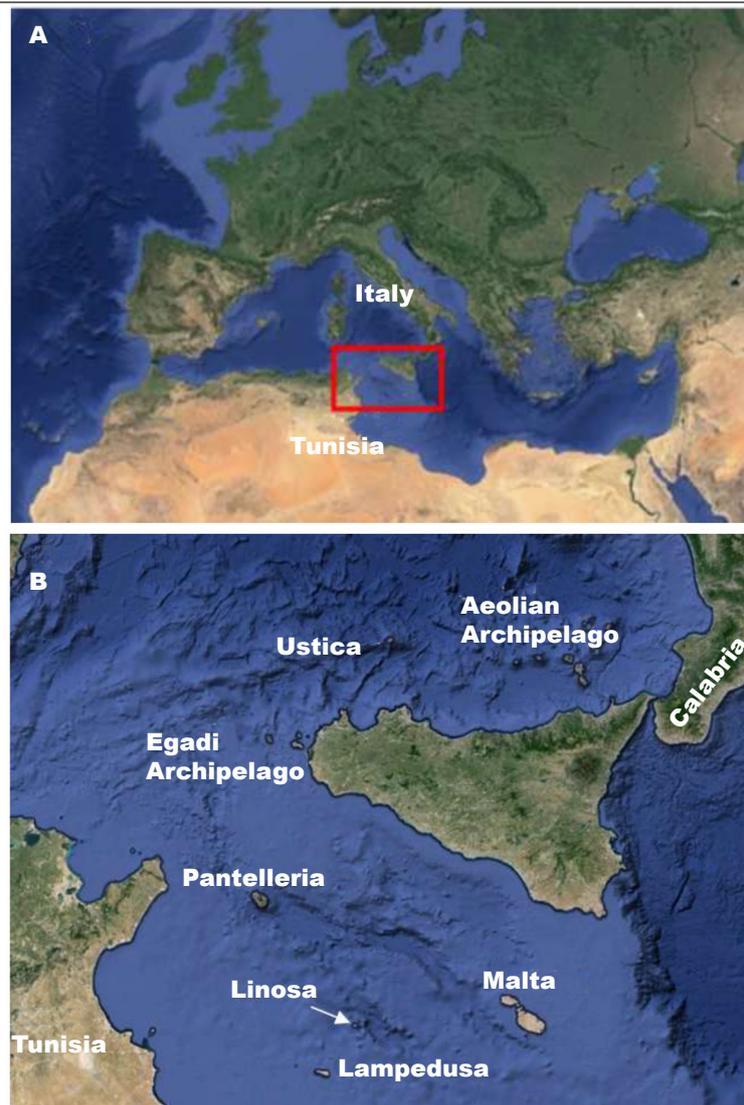


Fig. 1. Study area.

Fig. 1. Zona de estudio.

the Scarabaeoidea fauna of other possible source areas: Sicily, Calabria, Tunisia, Malta, Lampedusa and the Egadi archipelago (Favignana, Marettimo and Levanzo). These possible source areas, which include the nearest mainland areas and other non-volcanic islands in the region, were examined in two different scenarios (see 'Analysis and interpretation' heading). The main climatic and vegetation factors are reasonably homogeneous among the considered volcanic islands (Agnesi & Federico, 1995; Cicala, 1997; Pasta & La Mantia, 2003; Nesos, 2013). The climate of the volcanic islands is typically Mediterranean (Agnesi & Federico, 1995; Pasta & La Mantia, 2003; Blasi et al., 2005; Nesos, 2013). The vegetation, despite being altered to some extent by a long human presence,

is distinctly Mediterranean and the main natural environments are maquis and garrigue landscapes (Ronsisvalle, 1973; Baccetti et al., 1995; Pasta & La Mantia, 2003; Lo Cascio & Pasta, 2004; Nesos, 2013). Given the relative environmental homogeneity of the considered islands, it is assumed that the similarity in richness and composition should be mainly related with the role played by dispersal processes (Cadotte, 2006).

Data source and systematic group

The presence-absence data (see annex) were drawn from Arnone et al. (1995, 2001), Carpaneto et al. (2005), Agoglietta et al. (2006), Dellacasa & Dellaca-

sa (2006), Lo Cascio et al. (2006), Arnone, (2010), Fattorini (2010). The Tunisian data were taken from Baraud (1985) and Errouissi et al. (2009) and reviewed by Imen Labidi (pers. com., 2015) on the basis of comparisons with the collections Henry Normand and Muséum National d'Histoire Naturelle (Paris). Some data from the Egadi archipelago: *Euoniticellus fulvus* (Goeze, 1777), *Cheironitis irroratus* (Rossi, 1790), *Onthophagus taurus* (Schreber, 1759), *Calamosternus granarius* (Linnaeus, 1767), and *Calamosternus mayeri* (Pilleri, 1953) were provided by Marco Dellacasa (pers. com., 2014). The data for Malta were drawn from Pivotti et al. (2011).

Analysis and interpretation

There are several methods for reconstructing dispersal fluxes (Nathan et al., 2003). Some are complex and financially expensive but very informative (i.e., phylogeography), while others are simple and inexpensive but less accurate (i.e., pairwise comparisons derived from a presence/absence matrix in homogeneous areas; Legendre, 1986). In this study, we adopted the latter as a preliminary and exploratory strategy to evaluate the existence of any noteworthy patterns.

Data were analysed using the coefficient of dispersal direction DD_2 (Legendre & Legendre, 1984). This coefficient, rarely used in biogeographical analyses (but see: Legendre & Legendre, 1984; Bachraty et al., 2009; Borcard et al., 1995), measures the likelihood of species dispersal between two areas using species presence–absence data.

The formula of the DD_2 is:

$$DD_2(x_1 \rightarrow x_2) = \frac{2a}{2a + b + c} \frac{(b - c)}{a + b + c}$$

where a is the number of species that two regions have in common; b is the number of species found in x_1 but not in x_2 ; c is the number of species found in x_2 but not in x_1 . The first portion of the DD_2 coefficient is the Sørensen index of similarity, while the second portion measures the asymmetry in taxonomic composition. As Legendre & Legendre (1984) assert, 'the first portion states that unless two adjacent regions possess species in common, it would be difficult to think of these two faunas as deriving one from the other. The second portion creates the pictures of a fauna waiting at the border to invade an adjacent region; namely, the greater the number of species that inhabit an area, the greater the likelihood that this area acts as a source for neighbouring areas. Thus, DD_2 measures the likelihood that species have dispersed from x_1 to x_2 (b larger than c). A negative value (c larger than b) indicates that, if dispersal occurred, species might have migrated from x_2 to x_1 (Legendre & Legendre, 1984). In summary, the quantity $(b - c)$ would indicate the direction of dispersal flux, while the DD_2 value, which reacts to both the similarity and the asymmetry between areas, would estimate flux intensity (Bachraty et al., 2009). We chose to use the DD_2 index because, in analysing the possible dispersal fluxes, we think that presence is more important than supposed absence, and then we

decided to give double weight to the common species. This choice also allowed us to limit the biases and inconveniences caused by possible local extinctions.

To evaluate the dispersal fluxes, we divided the circum–Sicilian volcanic islands into two groups: north of Sicily (Aeolian Islands + Ustica) and south of Sicily (Pantelleria and Linosa). Then we hypothesized two colonization scenarios: the first excluding any continental islands as possible sources, and the second including continental islands as possible source areas (table 1). Of all the possible source areas (significant values of DD_2), we considered only those with the highest value of DD_2 as being likely source areas, since this value indicates a greater intensity of flux. When two or more possible source areas had a relative difference in the DD_2 value of less than 5%, they were both discussed as possible equivalent source areas.

The McNemar test was used to test the null hypothesis that there is no asymmetry between two areas ($H_0: b = c$). We used a two-tailed test of significance setting the probability of a type I error at $\alpha = 0.05$. The coefficients were calculated for each pair of areas. The coefficients DD_2 were calculated using the function `bgdispersal` of the Vegan Package (Oksanen et al., 2012) for the software R (R Development Core Team, 2011).

In order to identify the possible dispersal routes by the use of DD_2 coefficient, four assumptions were made. First, the volcanic islands were originally empty. The fauna and flora now present in these areas are necessarily dispersed from other source areas. This assumption is consistent with the geological history of the concerned islands. Indeed, they have originated from volcanic events in the period between 1,000 and 90 Kyr and it is impossible that they had an *ab origine* fauna. Second, the past dispersal events have necessarily left marks on the present communities (Legendre & Legendre, 1984; Borcard et al., 1995; Bachraty et al., 2009). Third, dispersal comes from areas of high to low taxonomic richness (Legendre & Legendre, 1984; Borcard et al., 1995; Bachraty et al., 2009). And fourth, given the strong homogeneity of the environmental parameters of the islands, the similarity in the biodiversity pattern and fauna between islands should be mainly related to dispersal processes.

Results

In total, through the literature review, we identified 176 dung beetle species as being present in the study area: 18 Geotrupidae, 53 Scarabaeidae, and 105 Aphodiidae. On the volcanic islands alone, 48 species are reported: 3 Geotrupidae, 24 Scarabaeidae, and 21 Aphodiidae. The species richness of the volcanic islands ranges from 35 (Vulcano island) to one (Panarea island). The species with the highest frequency in the volcanic islands is *Thorectes intermedius* (eight islands; see annex).

Tables 2 and 3 show the results of DD_2 fluxes with their McNemar and probability values. Figures 2 and 3 show these results graphically. The dispersal

Table 1. Context and scenario (S) in evaluating hypothetical dispersal fluxes to the volcanic islands:
* Continental islands.

*Tabla 1. Contexto y supuestos utilizados (S) en la evaluación de los hipotéticos flujos de dispersión hacia las islas volcánicas: * Islas continentales.*

Context	S	Target islands	Possible source areas
North of Sicily	1	Lipari, Salina, Vulcano, Stromboli, Filicudi, Alicudi, Panarea, Ustica	Sicily, Calabria, Lipari, Salina, Vulcano, Stromboli, Filicudi, Alicudi, Panarea, Ustica
North of Sicily	2	Lipari, Salina, Vulcano, Stromboli, Filicudi, Alicudi, Panarea, Ustica	As above + Egadi islands (Favignana*, Levanzo*, Marettimo*)
South of Sicily	1	Pantelleria, Linosa	Sicily, Tunisia, Pantelleria, Linosa
South of Sicily	2	Pantelleria, Linosa	As above + Egadi Islands (Favignana*, Levanzo*, Marettimo*), Malta*, Lampedusa*

patterns in the north of Sicily are equivalent in both scenarios with both Lipari and Vulcano acting as major source areas (three fluxes each) followed by Sicily (two fluxes) and Salina (one flux) (tables 2, 3; figs. 2, 3). Both scenarios show two equivalent fluxes towards Alicudi (Lipari and Vulcano).

Results in the Sicily Channel (south of Sicily) differ depending on the scenario. In the first scenario, Tunisia acts as a major source area (two fluxes), followed by Sicily (one flux). Linosa has two equivalent fluxes starting from Tunisia and Sicily, while the flux into Pantelleria indicates that it was probably colonized by Tunisian fauna. In the second scenario, Malta acts as a major source area (two fluxes) followed by Tunisia (one flux). Pantelleria shows two equivalent fluxes starting from Malta and Tunisia. Linosa was colonized by Maltese fauna (one flux).

Discussion

This study focused on the hypothetical dispersal routes of dung beetles in the circum-Sicilian volcanic islands. The survey was conducted applying the DD_2 coefficient of dispersal direction (Legendre & Legendre, 1984), a method that highlights the most probable routes of colonization considering the entire assemblages of each area.

It is interesting to note that the distribution of dung beetles on the circum-Sicilian volcanic islands could be the result of a coherent dispersal process rather than due to chance. This is corroborated by the fact that all DD_2 major fluxes had a significant value according to the McNemar test. In the north of Sicily, the dispersal fluxes led towards Vulcano and Lipari. These two islands thus acted as core source areas for the other islands (except Panarea,

which was colonized from Salina). The flow linking Ustica to Lipari suggests that the former was most likely colonized from the latter, noteworthy results since these islands are 150 km apart and Ustica is just 54 km away from Sicily. A chromosomal study (Colomba et al., 1995) about *Thorectes intermedius* populations of the mainland Sicily, Marettimo (Egadi Islands), Caprera (Sardinia) and Ustica revealed, as one would expect, that the populations of Ustica seem to be related to those of mainland Sicily. However, this study did not take into account the population of intervening areas, such as the Aeolian archipelago, as we did. The same is true for Alicudi, Filicudi, and Stromboli, all of which would have been colonized from Vulcano and Lipari, again acting as core source areas, as opposed to being targeted from their nearest neighbour in a stepping-stone fashion.

Although the cluster analysis used by Fattorini (2010) to examine the similarity of island assemblages does not allow to determine the direction of dispersal, our results are in agreement with some of those established by this author: Salina and Panarea are grouped together (see figure 3 in Fattorini, 2010), and in our work Salina is the source for Panarea. In the alternative solution of Kulczynski 2 (Fattorini, 2010: 1066), Salina was grouped with Lipari and Vulcano, and Lipari appears as the source of dung beetles for Salina. In Fattorini's Jaccard results, Alicudi is related to the Vulcano and Lipari group, and our results confirm this pattern with Alicudi displaying two equivalent fluxes departing from Lipari and Vulcano. In the Sicily Channel, Linosa has three equivalent fluxes, two in the first scenario and one in the second, with three possible source areas (Malta, Sicily, and Tunisia). Pantelleria has two equivalent fluxes (Tunisia in the first and second scenarios, and Malta in the second). Linosa is centrally located in the Sicily

Table 2. Results of coefficient of dispersal direction DD_2 (scenario 1): DD_2 . DD_2 value; M. McNemar value; P. McNemar probability (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$).

Tabla 2. Resultados del coeficiente de dirección de la dispersión DD_2 (supuesto 1): DD_2 . Valor DD_2 ; M. Valor McNemar; P. Probabilidad McNemar (* $P < 0,05$; ** $P < 0,01$; *** $P < 0,001$; **** $P < 0,0001$).

Dispersal flux	DD_2	M	P
Lipari → Ustica	0.21	14.36	***
Vulcano → Alicudi	0.24	30.97	****
Lipari → Alicudi	0.23	13.21	***
Vulcano → Filicudi	0.21	22.89	****
Sicily → Lipari	0.29	85.94	****
Salina → Panarea	0.27	4.93	*
Lipari → Salina	0.28	24.28	****
Vulcano → Stromboli	0.27	38.14	****
Sicily → Vulcano	0.33	69.70	****
Sicily → Linosa	0.14	104.97	****
Tunisia → Linosa	0.14	143.49	****
Tunisia → Pantelleria	0.18	137.94	****

Table 3. Results of coefficient of dispersal direction DD_2 (scenario 2): DD_2 . DD_2 value; M. McNemar value; P. McNemar probability (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$).

Tabla 3. Resultados del coeficiente de dirección de la dispersión DD_2 (supuesto 2): DD_2 . Valor DD_2 ; M. Valor McNemar; P. Probabilidad McNemar (* $P < 0,05$; ** $P < 0,01$; *** $P < 0,001$; **** $P < 0,0001$).

Dispersal flux	DD_2	M	P
Lipari → Ustica	0.21	14.36	***
Vulcano → Alicudi	0.24	30.97	****
Lipari → Alicudi	0.23	13.21	***
Vulcano → Filicudi	0.21	22.89	****
Sicily → Lipari	0.29	85.94	****
Salina → Panarea	0.27	4.93	*
Lipari → Salina	0.28	24.28	****
Vulcano → Stromboli	0.27	38.14	****
Sicily → Vulcano	0.33	69.70	****
Malta → Linosa	0.28	24.45	****
Tunisia → Pantelleria	0.18	137.94	****
Malta → Pantelleria	0.18	12.32	***

Channel, lying 120 km from Malta, 160 km from Sicily, and 165 km from Tunisia. Our results seem to reflect this geographical centrality, with no specific source area with major importance. Pantelleria seems to be more related with Tunisia, 70 km away. However, Malta (distance 200 km to Pantelleria) also seems to have played a role as source area. The importance of North Africa for Pantelleria is corroborated by studies carried out on other taxa. Magnano & Osella (1973), for example, reported that the curculionido-fauna of Pantelleria have the highest number of species with North African affinities compared to all other circum-Sicilian islands.

Our results do not strictly support the stepping-stone model which supports dispersal from one island to its nearest neighbour. Rather, north of Sicily, Lipari and Vulcano islands might have acted as core source areas; while in the Sicily Channel, Linosa would have been the favourite target area and Pantelleria would have had two source areas (Tunisia and Malta) that are very far apart. Furthermore, the most frequent species in the volcanic islands is *Thorectes intermedius*, a flightless species unable to survive for long periods in contact with sea water (Zunino, unpublished raw data; Colomba et al., 1995). Thus, the maintenance of a viable dung beetle population on far-away islands was necessarily linked to the presence of humans and

domestic mammals from which to draw the manure necessary to feed and nest. Indeed, although some species are polyphagous, they need dung for nesting and larvae development (Palestrini & Zunino, 1985; Verdú et al., 2007).

In view of these results, we propose that human movement was the principal factor accountable for dung beetle dispersal resulting in the colonization of the circum-Sicilian islands. Human activity and movement have played an important role as a medium for animal and plant dispersal (Pimentel, 2001; Forcina et al., 2015). Pimentel (2001) estimates that since the origin of farming (10,000 years ago), humans moved more than 400,000 species from one region of Earth to another. This phenomenon was particularly intense in the Mediterranean basin and its islands and increased as farming spread into this region (starting ca. 7,500 years ago) (Blondel & Vigne, 1993; Masseti, 1998; Blondel, 2006; Masseti & De Marinis, 2008; Vigne, 2014). The dispersal fluxes we have identified are in broad agreement with the ancient human colonization of the islands. In general, the circum-Sicilian islands were colonized directly from Sicily but, in the case of the Aeolian Islands, Lipari has played a role as main source area in the human colonization of the archipelago since the Neolithic Age (ca. 5,000 BC). There is limited evidence of settlement on Vulcano

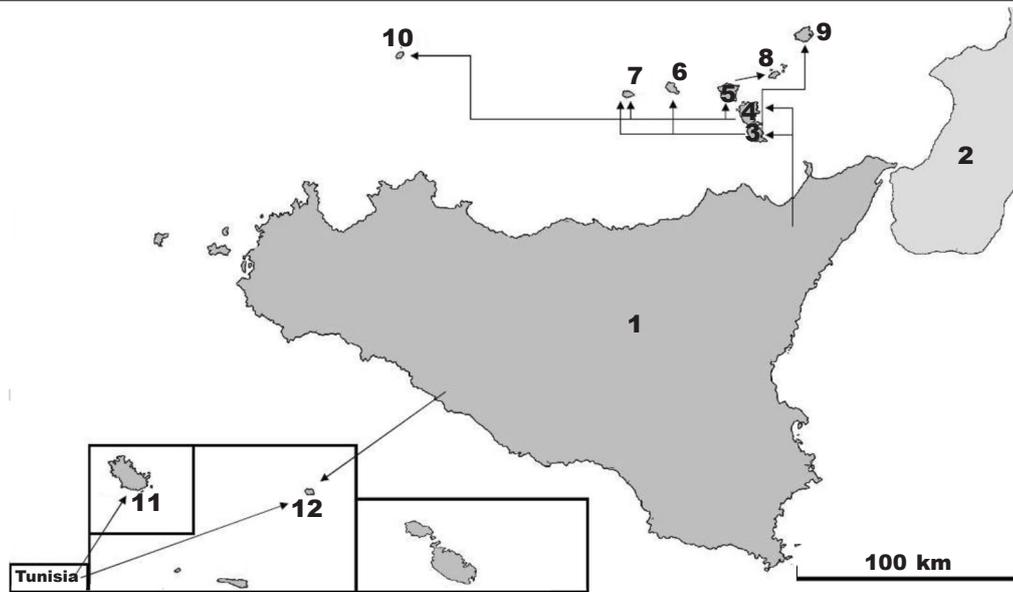


Fig. 2. Potential dispersal fluxes (→) for each volcanic island (scenario 1): 1. Sicily; 2. Calabria; 3. Vulcano; 4. Lipari; 5. Salina; 6. Filicudi; 7. Alicudi; 8. Panarea; 9. Stromboli; 10. Ustica; 11. Pantelleria; 12. Linosa.

Fig. 2. Posibles flujos de dispersión (→) para cada isla volcánica (supuesto 1): 1. Sicilia; 2. Calabria; 3. Vulcano; 4. Lípari; 5. Salina; 6. Filicudi; 7. Alicudi; 8. Panarea; 9. Estrómboli; 10. Ústica; 11. Pantelaría; 12. Linosa.

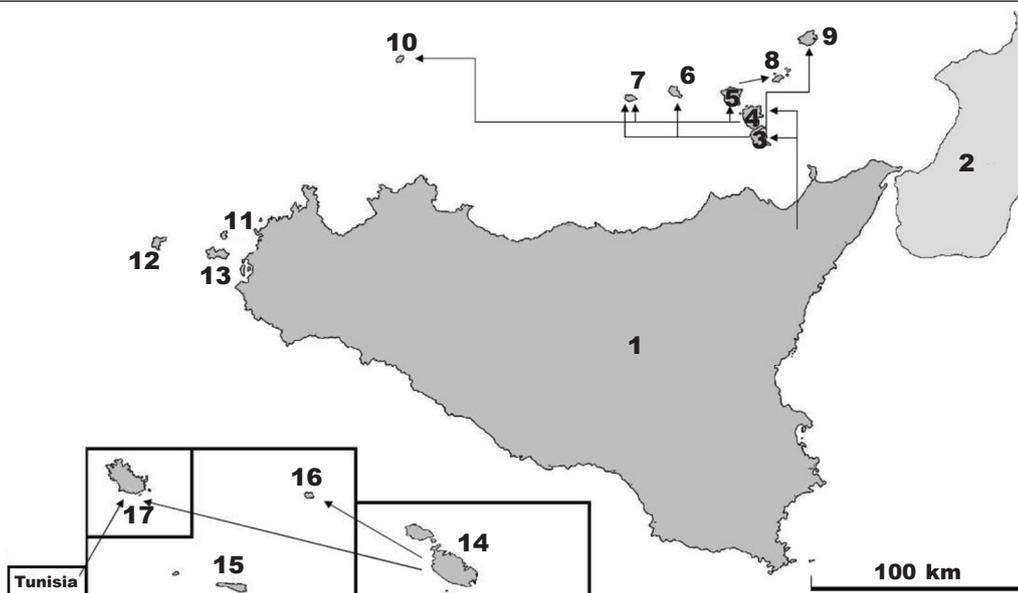


Fig. 3. Potential dispersal fluxes (→) for each volcanic island (scenario 2): 1. Sicily; 2. Calabria; 3. Vulcano; 4. Lipari; 5. Salina; 6. Filicudi; 7. Alicudi; 8. Panarea; 9. Stromboli; 10. Ustica; 11. Levanzo; 12. Marettimo; 13. Favignana; 14. Malta; 15. Lampedusa; 16. Linosa; 17. Pantelleria.

Fig. 3. Posibles flujos de dispersión (→) para cada isla volcánica (supuesto 2): 1. Sicilia; 2. Calabria; 3. Vulcano; 4. Lípari; 5. Salina; 6. Filicudi; 7. Alicudi; 8. Panarea; 9. Estrómboli; 10. Ústica; 11. Levanzo; 12. Marettimo; 13. Favignana; 14. Malta; 15. Lampedusa; 16. Linosa; 17. Pantelaría.

during the prehistoric period until the classical period, although sulphur and alum were probably extracted during the Bronze Age, and animals were possibly kept on the island by Lipari's earliest inhabitants, which would account for the similarities observed between the beetle fauna of the two islands. Owing to its agricultural potential and availability of desirable mineral resources (volcanic glass or obsidian), Lipari has been the only constantly occupied island in the Aeolian archipelago, with populations expanding and contracting on nearby islands, which underwent frequent episodes of abandonment (Bernabo Brea, 1958; Castagnino–Berlinghieri, 2011; Dawson, 2014). Contacts between the island of Ustica, first colonized by communities from Sicily in the Early Neolithic (6th–5th millennium BC) (Mannino, 1998), and the Aeolian Islands are already attested in the Early Bronze Age (early 2nd millennium BC) and become more frequent in the Middle Bronze Age (mid–2nd millennium BC), as seen from parallel developments in pottery styles (Spatafora, 2009, 2012). Obsidian from Pantelleria has been found in Neolithic contexts in Tunisia (Mulazzani et al., 2010: 57), in Malta, Linosa, and Lampedusa (Tykot, 1996), demonstrating links between coastal and island communities of the southern Mediterranean as early as the 7th and 6th millennia BC. The dung beetle data in this context support a flux from south to north in the Sicily Channel, a scenario which warrants further archaeological investigation and highlights the mutually beneficial nature of such an interdisciplinary study.

Given the distribution of Pantelleria obsidian on nearby Linosa, Malta, and the coastal areas of Tunisia (Tykot, 1996; Mulazzani et al., 2010), we can envisage a stop–over role for Pantelleria and nearby Linosa in the Sicily Channel, which would account for the distribution patterns observed for the dung beetles.

On the basis of archaeological data, the current coprophagous beetle faunas may have originated by dispersal mediated by the first island human settlements, through the movements of mammals, domestic and otherwise, that they were carrying. It is plausible that the first island communities also made frequent movements of animals between the islands, to take advantage of shifting local resources. The patterns detected would be the result of the distribution since the prehistoric period of human settlers with animals as well as of subsequent transfers between the islands. Arguably, the initial human exploration of the islands followed simple distance criteria. Instead, the decision to establish permanent settlements must have been influenced by other factors, such as the presence of mineral resources (flint and obsidian), in favour of landings, water resources, areas of pasture and arable land (the latter often a function of the size of the islands) as well as demographic, social and cultural factors (as was clearly the case in the Aeolian islands), with the establishment of preferential contacts between different communities, such as between Ustica and Lipari and Malta and Pantelleria (Dawson, 2011, 2014).

We should stress that our analysis considers the entire community of each island. It is therefore possible that some single species may have colonized a particular island following different routes from those

identified. Furthermore, these dispersal lines should not be considered as synchronous, but rather as the result of various events occurring over time. However, such events in different places and times must have left a trace in the present–day communities (Legendre & Legendre, 1984), decipherable according to our dispersal models in figures 2 and 3. This implicates that further investigation is indispensable to corroborate or refute our hypothesis. We suggest that phylogeographic studies may help describe with precision the spatial and temporal connections of dung beetle fauna in these volcanic islands, especially for the flightless species *Thorectes intermedius*.

Conclusion

According to our study, the dung beetle communities of the circum–Sicilian volcanic islands display dispersal fluxes that do not strictly underlie the stepping–stone dynamics. This is especially true for the islands to the north of Sicily, where Lipari and Vulcano act as core source areas for dispersal routes. In the Sicily Channel, small and faraway Linosa was colonized from Tunisia, Malta and Sicily, while Pantelleria was principally colonized by fauna from Tunisia and to a lesser extent from Malta. These results, together with the fact that a flightless species, *Thorectes intermedius*, is most frequently found on these islands, are supported by archaeological patterns in the islands' human colonization, suggesting a strong human contribution to the genesis of the dung beetle fauna of the circum–Sicilian volcanic islands.

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