

Biogeographical patterns of the genus *Merodon* Meigen, 1803 (Diptera: Syrphidae) in islands of the eastern Mediterranean and adjacent mainland

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Abstract. 1. The objective of this study was to obtain a biogeographical perspective on the hoverfly genus *Merodon* (Diptera, Syrphidae) based on data from 32 islands in the Aegean and Ionian archipelagoes *vis-à-vis* the adjacent mainland. In this part of the world, the genus comprises 57 species, out of more than 160 species described worldwide.

2. The importance of eco-geographical variables (area, elevation, distance to the nearest island and distance to the nearest mainland) and the species–area relationship (SAR) were studied in order to explain patterns of species richness. All tests supported the dynamic equilibrium concept.

3. The area and distance to closest island were found to be the most important drivers of species richness on the Aegean and Ionian archipelagoes. Out of three SAR models evaluated in this study, the exponential function fitted our data best. It was found that a power model with no intercept value ($C = 1$) performed even better by using symbolic regression for non-linear equation optimisation.

4. The cluster and null-model analyses performed to detect inter-island similarities and origins of the insular *Merodon* fauna indicated a clear influence of colonisation history of the species on different islands.

5. The results imply that the current distributions of *Merodon* species in the study area exhibit the combined effects of historical and present-day processes.

Key words. Biogeography, distribution patterns, eco-geographical variables, hoverflies, islands, species–area relationship.

Introduction

The genus *Merodon* Meigen, 1803 (Diptera: Syrphidae: Eumerini), consisting of more than 160 species (Stähls *et al.*, 2009), distributed over the Palaearctic and

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Afrotropical biogeographical regions, is one of the most widespread and abundant hoverfly genera in the Mediterranean region (Dirickx, 1994). *Merodon* species are flower visitors and most probably, as most hoverflies, provide important ecosystem services as pollinators, both in continental and island systems (Pérez-Bañón *et al.*, 2003, 2007; Petanidou *et al.*, 2011). Most of the species are associated primarily with geophytes in various ways: the adults are involved principally in the pollination of flowers which they visit for nectar and pollen while the phytophagous larvae are associated with their bulbs or other storage organs to feed on, being restricted to areas rich in bulbous plants (Hurkmans, 1993; Popov, 2001; Ricarte *et al.*, 2008).

Islands are natural laboratories that are ideal for studies on species distribution patterns. A theoretical model accounting for the variation in species diversity on islands was provided by MacArthur and Wilson (1963, 1967). Their 'equilibrium theory of island biogeography' revolutionised scientific thought in ecological biogeography, explaining variation in species richness with area and geographical isolation as the primary determinants.

The Mediterranean region is considered to be one of the most geographically complex areas in the world, especially because of its archipelagoes, the richer and most emblematic being that of the Aegean (Blondel *et al.*, 2010). This archipelago consists of 7852 islands and islets, of which 95% are smaller than 1 km² (Triantis *et al.*, 2008). High species richness and endemism of the Aegean flora and fauna is the result of a combined influence of the adjacent mainland as source areas, a multifaceted geological history, and a diverse geomorphology (Lymberakis & Poulakakis, 2010). Furthermore, this region has been noted as the only one in the world comprising flora and fauna originating from three different geographical continents: Europe, Asia and Africa (Triantis *et al.*, 2008).

Numerous studies have investigated biogeographical patterns of particular invertebrate taxa in the Mediterranean region, and especially in the Aegean archipelago: terrestrial mollusks (Mylonas, 1982; Vardinoyannis, 1994; Welter-Schultes & Williams, 1999); terrestrial isopods (Sfenthourakis, 1996a,b; Sfenthourakis & Giokas, 1998; Gentile & Argano, 2005; Triantis *et al.*, 2008); centipedes (Stathi & Mylonas, 2000; Simaiakis *et al.*, 2005, 2012); ground spiders (Chatzaki *et al.*, 2002); beetles (Trichas & Legakis, 1987; Fattorini, 2002, 2006; Chatzimanolis *et al.*, 2003); and butterflies (Dennis *et al.*, 2000). Many of the studies considered both island area and isolation as important factors explaining the historical events in faunal diversity (Dennis *et al.*, 2000; Hausdorf & Hennig, 2005; Dapporto & Cini, 2007). Geological events also shaped the present distribution patterns of the species occurring in the Aegean archipelago to a large degree (e.g. Hausdorf & Hennig, 2005).

Due to a large number of islands of diverse sizes and distances from their adjacent continents or between them, and a very long history of human inhabitation, the Aegean archipelago has proved to be an excellent natural

system for analysing species diversity and distribution. The archipelago also represents one of the world's hotspot areas for pollinators, both bees and hoverflies (Potts *et al.*, 2006; Vujić *et al.*, 2007, 2012, 2013; Nielsen *et al.*, 2011; Radenković *et al.*, 2011).

The Aegean islands have a particularly complex history, as they were in contact with each other and with their neighbouring land masses for various periods at different times during Plio-Pleistocene (Strid, 1970; Dermitzakis & Papanikolaou, 1981). Numerous studies mostly supported the hypothesis of a relictual character of the different animal groups: terrestrial isopods (Sfenthourakis, 1996a), land snails (Welter-Schultes & Williams, 1999) and tenebrionid beetles (Fattorini, 2002). Such a relict distribution pattern cannot be expected in the case of *Merodon* species, which are good fliers and potentially highly mobile insects. Due to this mobility, the current species diversity and distribution patterns of *Merodon* species in the archipelago might therefore be the result of more recent colonisation events. This study tries to explain the observed distribution patterns of *Merodon* species by testing variables that are related to migration capacity, viz. the island size and the distance to the mainland.

Based on our comprehensive dataset collected from the eastern Mediterranean, the biogeographical patterns exhibited by *Merodon* species in the area were explored. The particular objectives of the study were to: (i) consolidate the knowledge of the distribution and species richness of the genus by assigning a zoogeographical classification to all species occurring in the eastern Mediterranean islands; (ii) elucidate which of the tested eco-geographical variables (i.e. area, elevation, distance to the mainland, distance to the nearest island) correlate and/or best explain the observed species richness and distribution; (iii) find the best model explaining the species-area relationship; (iv) examine the patterns of island faunal similarities among *Merodon* species; and (v) establish the relationship between each island's fauna and its possible origins.

Materials and methods

Surveyed area and sampling

The surveyed area is situated in the eastern Mediterranean and comprises 32 islands that are larger than 100 km² (Fig. 1). The study material was collected on 28 Aegean islands, three Ionian islands, Cyprus, as well as on the mainland of Greece, and the Aegean coast of the Anatolian Peninsula (Turkey) (Fig. 1, Table S1).

The paleo-geographical history of the study area, especially of the Aegean, is very complex. Today's archipelago is situated in an active geological region, a subduction zone where the African plate moves under the Eurasian plate. The Aegean started to form about 13 million years ago (Mya) (Dermitzakis, 1990) with the breaking apart of a continuous landmass (Ägäis), which had appeared at

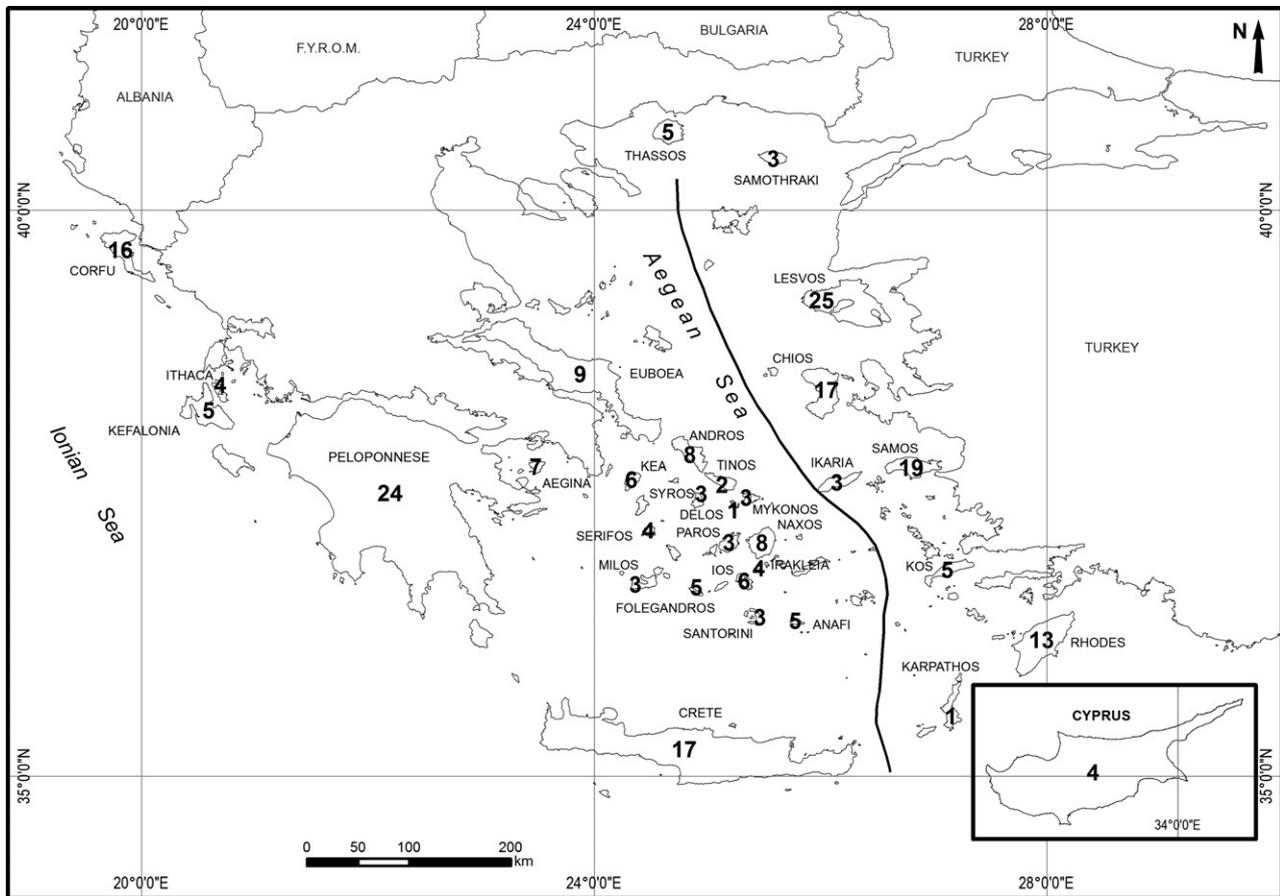


Fig. 1. Map showing the surveyed islands with the number of *Merodon* species shown on each island. Mid-Aegean dividing line drawn in black.

the northern coast of the Tethys Ocean during the early Miocene about 23 Mya (Lymberakis & Poulakakis, 2010). Tectonic, eustatic, and volcanic activity have been dynamically shaping the region and thus also affecting the species inhabiting it. Most of today's Aegean islands became isolated at least twice in their history, once during the Messinian salinity crisis (Krijgsman *et al.*, 1999) about 5 Mya ago and most recently after the Last Glacial Maximum (Perissoratis & Conispoliatis, 2003; Triantis & Mylonas, 2009) some 26 000 years ago. The islands of the archipelago vary significantly in maximum elevation, with the highest peak occurring on Crete (2456 m). Larger islands comprise complex relief patterns with mountains and gorges. Situated within a typical Mediterranean climate zone, most of the islands climax vegetation used to be Mediterranean open deciduous, conifer, and mixed forests (dominated by *Quercus* and *Pinus*) before the human-induced deforestation, most excessive during the classical times, e.g. Kouli (2012). More than 4500 years of human presence on most islands have led to habitat degradation and conversion (Blondel *et al.*, 2010). Thus, as a result of intensive grazing, logging and burning, original forest

vegetation remains only in small and often isolated pockets, with phrygana being the dominant type of vegetation nowadays (Blondel *et al.*, 2010). Phrygana, together with other semi-open arid rocky habitats rich in bulbous plant species, constitute the main habitats for *Merodon* species (Speight, 2013). Such *Merodon*-friendly habitats are widely distributed throughout the whole study area.

Data set

Species distribution data were based mainly on recent collections of *Merodon* from the study islands and the surrounding mainland areas (Greek and Anatolian Peninsulas). Collecting was carried out by hand-netting, pan-trapping, and Malaise trap setting between the years 2003 and 2014. The total number of specimens amounted to 8863 belonging to 53 species.

Additional data were obtained from museum collections and other repositories during several repeated visits to these facilities to check species taxonomy and record locality data. The visited facilities were: American Museum of

Natural History, New York, USA; Natural History Museum, London, UK; Faculty of Sciences, Department of Biology and Ecology, University of Novi Sad, Serbia; The Melissotheque of the Aegean, University of the Aegean, Mytilene, Greece; Muséum National d'Histoire Naturelle, Paris, France; Finnish Museum of Natural History, Zoology unit, Helsinki, Finland; Naturhistorisches Museum Wien, Austria; Nationaal Natuurhistorisch Museum, Leiden, Netherlands; World Museum Liverpool, UK; Zoologisches Museum of the Humboldt University, Berlin, Germany; and private collections (Martin Hauser collection, USA; Menno Reemer collection, The Netherlands; J. Smart collection, UK; John Smit collection, The Netherlands; Axel Szymank collection, Germany; Mike Taylor collection, UK; Van Weyer collection, The Netherlands). The number of *Merodon* records obtained from these collections amounted to 3245 belonging to 42 species, of which 25 were additional species.

The entire dataset consisted of 12 108 *Merodon* specimens or records belonging to 78 species. Out of these data, 57 *Merodon* species occurring on the 32 study islands were used in the analyses (Fig. 1, Table S1). As the Aegean islands and the adjacent mainland areas are tightly interconnected, 21 taxa occurring only on mainland areas were also stored in the data base, although these taxa were not considered in our analyses. Only the islands that were sampled for a minimum of three times during *Merodon* adult flight season and for a minimum of two collecting days per visit were included. Based on our extensive experience with *Merodon* in the entire Mediterranean area, the sampling effort conducted on the 32 study islands was sufficient to have recorded a very large proportion if not all species occurring on respective islands. To test efficiency in species sampling effort, species accumulation curves (plotting cumulative species numbers of against collecting days) were generated for each island (Fig. S1). They indicate that the sampling effort was sufficient, since saturation has been shown for most of the islands. The *Merodon* species lists presented here for the different islands are therefore considered nearly complete.

Zoogeographical classification of *Merodon* species occurring in the eastern Mediterranean

All *Merodon* species analysed (Table S1) were assigned to seven zoogeographical categories (Table 1): three of them (viz. Balkan, Anatolian, and widely distributed species) are according to Fattorini (2002), the remaining four were added to cover all the observed distribution patterns of our *Merodon* database. The zoogeographical classification also included species already recognised as taxa new to science based on our morphological and/or molecular evidence, but not yet taxonomically formalised as indicated by the addition of the epithet 'aff.'. In some cases, groups of closely related new taxa that are morphologically very similar are identified as 'aff. 1, 2, 3'

(Table 1). These taxa will be described as species new to science in separate studies.

Eco-geographical variables

Data on island area and maximum elevation were provided by Hellenic Military Geographic Service (HMGS), Institute for the Management of Information Systems of the 'Athena' (<http://geodata.gov.gr/geodata>) and Laboratory of Cartography and Geoinformatics of the Department of Geography of the Aegean University. For each island included in the analyses, the smallest distance from its coastline to the nearest adjacent mainland and to the nearest island larger than 1 km² was measured using Google Earth software (Table S1).

Data analysis

Species richness drivers. The following eco-geographical variables were chosen and tested as predictors of *Merodon* species richness on the eastern Mediterranean islands: log (area), elevation, distance to the nearest island and distance to the nearest mainland. The Pearson product-moment correlation coefficient was used to estimate the correlations among eco-geographical variables and the species richness. Linear regression with richness as dependent variable was then performed. The best subset among all possible combinations of independent variables was chosen according to the corrected Akaike's Information Criterion (AICc) values using the R package MuMIn (Barton, 2015) after excluding variables with variance inflation factor VIF >5 using R package car (Fox & Weisberg, 2011). Variation partitioning was used to quantify the individual and combined contributions of the different variables using R package vegan (Oksanen *et al.*, 2015). Finally, using symbolic regression (SR, Cardoso *et al.*, *subm.*), an attempt was made to find an alternative non-linear model that would better fit the species richness of islands depending on the same four variables. The software Eureqa (Schmidt & Lipson, 2015) was used for SR function discovery. This was compared with the linear model above using AICc in R (R Core Team, 2015).

Species–area relationship. The species–area relationship was investigated in this study using three different models (for a review on species–area functions see Dengler, 2009; Triantis *et al.*, 2012). These mathematical models have been widely used for species–area analysis, but the best-fit model for the specific data can usually be determined empirically (cf. Connor & McCoy, 1979).

The models used in this investigation were the linear ($S = C + zA$), exponential ($S = \log C + z \log A$), and power ($S = CA^z$) models (Dengler, 2009). In all models, S is the species richness, A is the area, and C and z are constants representing the intercept (C) and slope (z). Models were fitted using the R package BAT (Cardoso *et al.*, 2015) and compared based on both r^2 and AICc.

Table 1. Zoogeographical categories of eastern Mediterranean *Merodon* species.

Category	Distribution range	<i>Merodon</i> species
Balkan (BAL) 12 species	Species distributed over the Balkans and eastern Mediterranean Islands, but not in the Anatolian Peninsula	<i>Merodon abberans</i> , <i>M. albifasciatus</i> , <i>M. aureus</i> , <i>M. aff. aureus</i> 1, <i>M. auripes</i> , <i>M. aff. bessarabicus</i> , <i>M. clavipes</i> , <i>M. equestris</i> , <i>M. minutus</i> , <i>M. moenium</i> , <i>M. natans</i> , <i>M. aff. puniceus</i>
Anatolian (ANA) 19 species	Species present in the Anatolian Peninsula and on the eastern Mediterranean Islands, but absent in the Balkan Peninsula	<i>Merodon aff. albifasciatus</i> 1, <i>M. aff. albifasciatus</i> 2, <i>M. aff. avidus</i> , <i>M. aff. chalybeus</i> , <i>M. aff. constans</i> , <i>M. crassifemoris</i> , <i>M. aff. desuturinus</i> , <i>M. hamifer</i> , <i>M. nanus</i> , <i>M. aff. nanus</i> , <i>M. aff. nigratarsis</i> , <i>M. papillus</i> , <i>M. planiceps</i> , <i>M. pulveris</i> , <i>M. puniceus</i> , <i>M. sapphous</i> , <i>M. spinitarsis</i> , <i>M. telmateia</i> , <i>M. testaceus</i>
Levant (L) one species	Occurring in the Levant (area in Southwest Asia covering Cyprus, Israel, Jordan, Lebanon, Palestinian Territories, Syria and Hatay in Turkey)	<i>Merodon hirtus</i> (Israel, Cyprus)
Western Mediterranean (WM) two species	Predominantly western distribution but also found on single islands in the eastern Mediterranean	<i>Merodon femoratus</i> (only on Crete), <i>M. trochantericus</i> (Corfu)
Island endemic (END) seven species	Local species restricted to one or two islands	<i>Merodon caeruleus</i> (Rhodes and Crete), <i>M. aff. aureus</i> 2 (Peloponnese), <i>M. aff. aureus</i> 3 (Naxos), <i>M. aff. aureus</i> 4 (Andros), <i>M. aff. sapphous</i> 1 (Rhodes), <i>M. aff. sapphous</i> 2 (Crete), <i>M. aff. sapphous</i> 3 (Cyprus)
Continental and large island (COL) 13 species	Comprising species present on both peninsulas and islands larger than 420 km ² (like Naxos, Samos, Lesvos, Cyprus, Crete, Euboea)	<i>Merodon alagoesicus</i> , <i>M. chalybeatus</i> , <i>M. clunipes</i> , <i>M. erivanicus</i> , <i>M. femoratoides</i> , <i>M. funestus</i> , <i>M. italicus</i> , <i>M. latifemoris</i> , <i>M. loewi</i> , <i>M. nigratarsis</i> , <i>M. pruni</i> , <i>M. serrulatus</i> , <i>M. velox</i>
Widely distributed (WD) three species	Species distributed over both peninsulas and the eastern Mediterranean Islands. These taxa also occur on small islands	<i>Merodon albifrons</i> , <i>M. aurifer</i> , <i>M. avidus</i>

In addition, and again using symbolic regression, an attempt was made to find a novel model that would outperform the hitherto described, using area as the single explanatory variable. The software Eureqa was again used for SR function discovery. The new model was compared with all previous using AICc.

Similarity of the Merodon fauna between islands. The Sørensen Similarity Index was used to examine the similarity of the *Merodon* fauna among the study islands. In order to obtain a clear picture of similarities and connections not only among the islands, but also among groups of islands, a hierarchical cluster analysis (UPGMA) was performed using BAT and core R functions. The statistical support to groups in the dendrogram was tested using the kgs penalty function (Kelley *et al.*, 1996), whose minimum value identifies consistent and distinct clusters of sites. The R package mapeer was used for kgs analysis (White & Gramacy, 2012).

Origins of island faunas. To test if the origins of the fauna of each island could be significantly related with Western or Eastern faunas, all species were primarily divided into the four main categories: Wide distribution,

Balkan (western), Anatolian + Levant (eastern) or Island endemics. The number of western and eastern species was quantified for each island. Using a null-model approach, the numbers expected if species were randomly spread over all the islands were tested, with the total species richness per island being kept constant. The observed and expected values were compared and the *P*-values calculated.

Results

Species richness drivers

The *Merodon* species richness per island showed a positive correlation with log (area) ($r = 0.643$, $P < 0.001$), as well as elevation ($r = 0.529$, $P = 0.002$). On the other hand, species richness was negatively correlated with distance to the nearest mainland ($r = -0.407$, $P = 0.021$) and no statistically significant correlation was found with distance to the nearest island ($r = -0.109$, $P = 0.553$).

The best linear model according to AICc and after excluding elevation due to high vif (due to correlation

with area) was ($r^2 = 0.538$, $AICc = 99.618$):

$$S = -7.360 + 2.779 \log A - 0.057 Di$$

Where S = species richness, A = area and Di = distance to nearest island. The variable Dm (distance to the mainland) was excluded from this model. The variation partitioning (Fig. 2) reveals that in fact the individual contribution of Dm is minimal, as its total contribution is mostly shared with A . Area is by far the factor individually contributing most to explained variance, followed by Di .

The symbolic regression method did find a non-linear model that outperforms any linear model ($r^2 = 0.706$, $AICc = 85.181$):

$$S = 1.394^{\log A} + \log A / \log Dm - \sqrt{Di}$$

In this case, Di is deemed important to the model after square root transformation, as is the interaction between A and Dm , both after log transformation.

Species–area relationship

The best fitting SAR (species–area relationship) model of the three tested (linear, exponential and power) was the exponential ($r^2 = 0.414$, $AICc = 109.665$):

$$S = -5.548 + 2.314 \log A$$

The SR method did, however, find a better fitting equation, a simplification of the power model without the intercept (equivalent to $c = 1$) ($r^2 = 0.388$, $AICc = 108.576$):

$$S = A^{0.313}$$

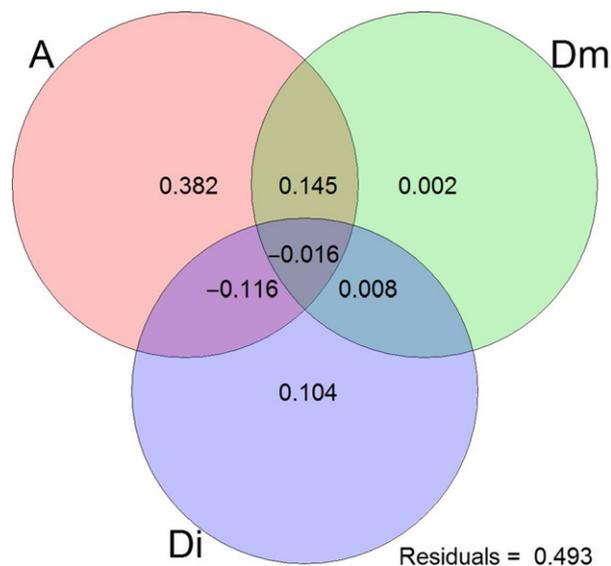


Fig. 2. The variation partitioning: A – area; Di – distance to nearest island; Dm – distance to the nearest mainland.

With one less fitting parameter this new model explains almost as much variance as the exponential.

Similarity of the *Merodon* fauna between islands and origins of island faunas

The cluster analysis followed by separation of groups using kgs identified six distinct clusters (Fig. 3). Our results showed that *Merodon* faunas of big islands that are situated closer to the Anatolian mainland and belong to the groups of North Aegean or the Dodecanese Islands (Lesvos, Chios, Samos Rhodes and Kos) cluster together. Joining them are Cyprus and the Ionian islands Ithaca and Kefalonia. Most of the Cycladic islands form separated cluster which also includes Aegina and Euboea. Another cluster brings together group of small Cycladic islands and joining them are Peloponnese, Corfu (Ionian island), Crete and northern Aegean island of Thassos. Cycladic Islands of Syros and Delos clustered independently. The last cluster brings together Cycladic island Serifos, Dodecanese island Karpathos, and one of North Aegean (Ikaria). Samothraki, a small, fairly isolated North Aegean island is the most independent and did not cluster with any of the study islands, but as a separate first off-shoot in the dendrogram.

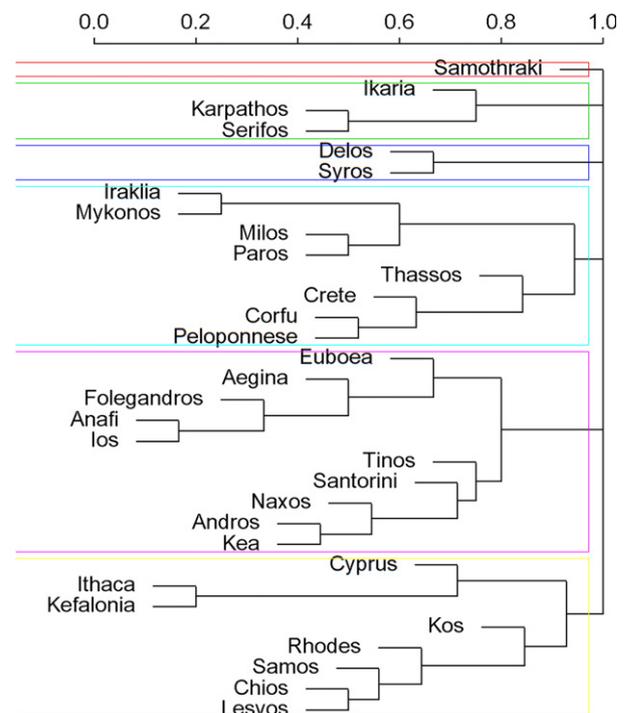


Fig. 3. The relationships of the study islands based on *Merodon* species composition, obtained by Sørensen Similarity Index and cluster analysis.

Regarding the zoogeographical classification of the taxa and their presence on individual islands (Table S2), faunas of some islands are examples of how the faunal compositions formed from the different distributional elements, but none of the islands harbour taxa from all seven zoogeographical categories. The most diverse islands harbouring species of different zoogeographical origin are Crete with six, Naxos with five, and some islands (Rhodes, Corfu, Andros) encompassing a *Merodon* fauna of four different distribution categories (the latter recorded for the Peloponnese as biological island *sensu* Blondel *et al.*, 2010, Table S1). Some other islands have very high numbers of species belonging to only few zoogeographical categories: Lesvos (25 species from three categories), Chios (17 species from three categories), and Samos (19 species from three categories).

The four main zoogeographical categories of eastern Mediterranean *Merodon* species on the study islands (Table S3) are presented on Fig. 4. Of the endemic species, 62% occur on the more isolated islands situated on the southern border of the eastern Mediterranean islands, i.e. Cyprus, Rhodes and Crete, while Peloponnese and

eastern Cycladic islands Andros and Naxos harbour one different endemic taxon each.

The fauna from seven islands can be considered as predominantly Western: Anafi, Corfu, Crete, Euboea, Ios, Peloponnese and Samothraki. Mainly, eastern origins could be attributed to three islands: Delos, Lesvos and Samos. The fauna from the other 22 islands could not be significantly related to any specific origin, although the typically low number of species does make it hard to reach significance.

Discussion

This study shows that the eastern Mediterranean hoverfly fauna of the genus *Merodon* is mainly influenced by the current eco-geographical variables, namely island area and distance to the nearest island. This supports the equilibrium model which predicts that species richness increases with island area and decreases with distance from the source pool (MacArthur & Wilson, 1967). A similar pattern was also noted in a comparable study on the Aegean butterfly fauna by Dennis *et al.* (2000). In this study, the

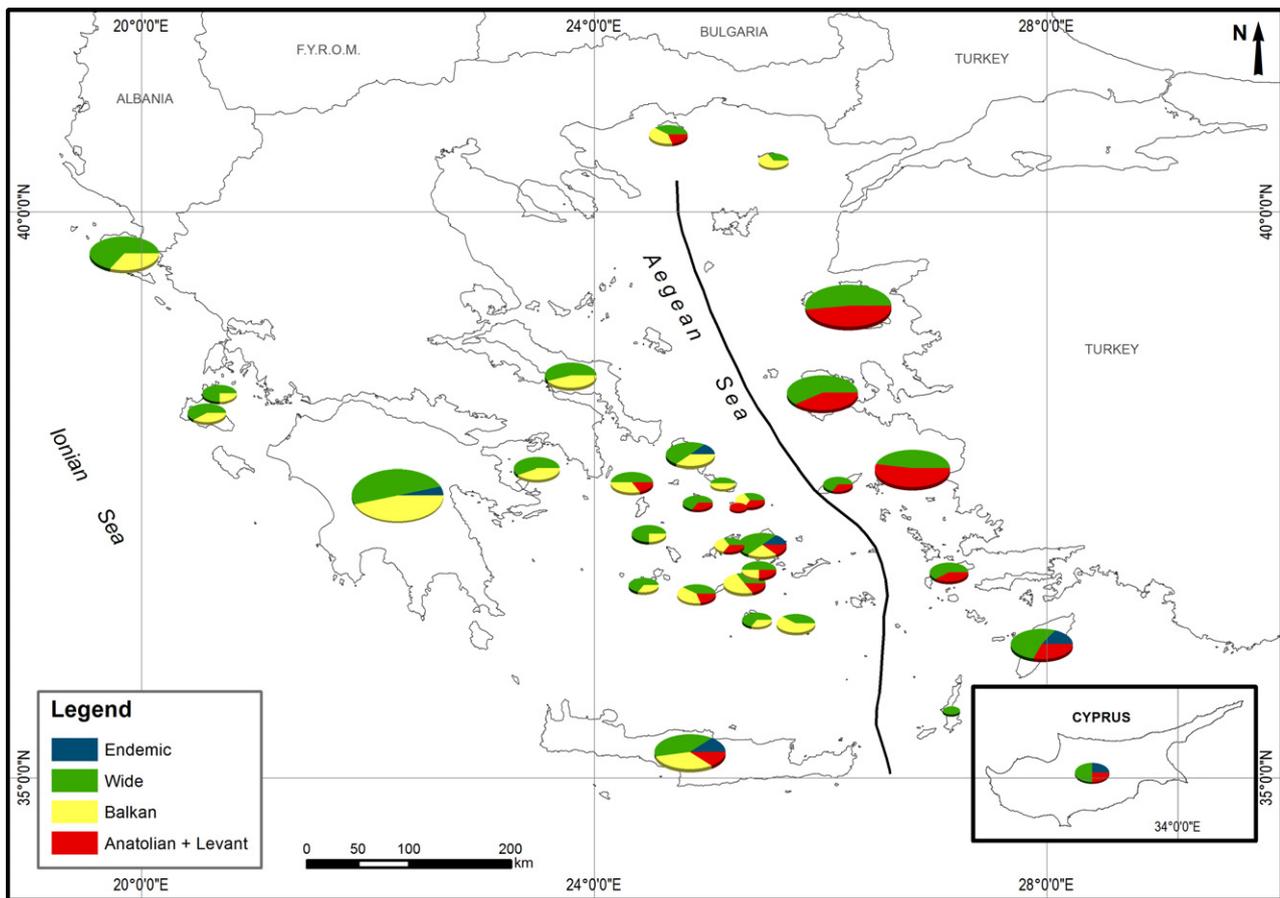


Fig. 4. Four main zoogeographical categories of eastern Mediterranean *Merodon* species on investigated islands. The size of each pie is analogous to the total diversity (number) of *Merodon* species of the island. Mid-Aegean dividing line drawn in black.

variation partitioning analysis (Fig. 2) has shown that contribution of the distance to the nearest mainland is mostly shared with island area, which is the factor individually contributing most to the explained variance, followed by distance to the nearest island. Although elevation showed positive correlation with species richness, this factor has been excluded in further analyses because of its high correlation with area. Habitat heterogeneity on islands often appears as a result of variation along an elevational gradient and the underlying environmental factors such as temperature and precipitation, thus elevation can be considered as at least a rough indicator of habitat heterogeneity (Muhlenberg *et al.*, 1977; Nussbaum, 1984; Steinbauer *et al.*, 2013). It is not easy to disentangle the effects of island area and elevation since they are confounded by the positive correlation between them; however, positive correlation of these variables with species richness can indicate the importance of increased habitat heterogeneity in explaining species area relationships. These results highlight the importance of contemporary geographical features in governing species richness.

Whether on islands or continents, the species–area relationships are of crucial biogeographical importance (Whittaker & Fernández-Palacios, 2007). Indeed, studies on island biogeography have shown that species with relict patterns are not in accordance with the equilibrium models because species richness in such relict faunas is not influenced by the distance of the island from the source pool (Fattorini, 2002). On the other hand, some faunal patterns are better explained by present ecological and geographical factors (area, isolation) than by historical geographical changes (Dapporto & Cini, 2007). The models tested in our study clearly showed a positive relationship between species richness and island area. The exponential and power function models (Báldi & Kisbenedek, 1999; Lobo & Martin-Piera, 1999) fitted our data best. The latter agrees with Dengler (2009) and Triantis *et al.* (2012), who suggested that the power function was the most appropriate model for different species–area data, based both on theoretical considerations and literature data. In their comprehensive study of the island species–area relationship, Triantis *et al.* (2012) have confirmed the scale dependence of the shape of this relationship, i.e. SAR form variation could be related to the array of causal mechanisms and processes (e.g. evolutionary history, habitat diversity effect, random placement and area-based incidence functions) that shape the ecological space available in an the archipelago and the geographical context within which islands are located. The majority of the islands studied here were larger than 70 km², and the observed relationship is in accordance with the hypothesis that larger islands tend to be more topographically diverse. This also results in complex habitats and thus more available niches for potential colonists leading to a higher number of species (MacArthur & Wilson, 1967; Lomolino *et al.*, 2010). Another hypothesis (MacArthur & Wilson, 1963, 1967) suggests that the

number of species increases with the island size due to the increase in the size of populations, which reduces the probability of extinction. Most probably both factors, habitat availability and increased abundance, have a role in shaping species richness.

In this study, islands with recorded endemic species are Andros, Crete, Cyprus, Naxos, Peloponnese and Rhodes. Crete and Cyprus are the largest and most isolated islands of the eastern Mediterranean, and both islands have been isolated since the Miocene (Sondaar & van der Geer, 2002). The long-term isolation along with their size and geographical separation could therefore be expected to support a high species diversity and endemism (Losos & Schluter, 2000; Whittaker & Fernández-Palacios, 2007; Losos & Ricklefs, 2009). Dennis *et al.* (2000) found that endemic butterfly species and subspecies were concentrated on larger southern islands (such as Cyprus, Chios, Crete, Karpathos and Rhodes) in the periphery of the eastern Mediterranean area, which is in accordance with our results. The Aegean endemic butterfly fauna is small, comprising only 5.2% of the occurring species (6 out of 116 species; Dennis *et al.*, 2000). It was found here that the percentage of endemic *Merodon* species in the eastern Mediterranean islands is more than twice the percentage of the butterfly fauna, namely 12.3% (7 of 57 species). Additionally, endemic *Merodon* species occur also on smaller islands of the Cyclades (Andros and Naxos) (Table S1), while no endemic butterflies were found on these islands (Dennis *et al.*, 2000). The observed percentage of *Merodon* endemism is in accordance with the level of plant endemics (12%) in the eastern Mediterranean (Dennis *et al.*, 2000).

Analyses of the origins of island faunas revealed that fauna of certain island could be considered as of eastern or western origins, which was in accordance with zoogeographical classification of the taxa and their presence on individual islands (Fig. 4, Tables S2 and S3). Namely, mainly eastern origins were attributed to islands Lesvos and Samos, which have approximately half of the *Merodon* species previously classified as Anatolian. On the other hand, fauna of Peloponnese, Corfu and Crete was shown to be predominantly western and these islands are characterised with the highest percentage of Balkan species. These results comply with those of the analysis of the similarity of *Merodon* fauna between islands, which clusters given islands in the dendrogram (Fig. 3).

Cluster analysis indicated dominant influence of historical factors in the *Merodon* distribution patterns. Although Pleistocene events, such as the lowering of the sea level and resulting land bridges between islands and islands/mainland have likely influenced the processes of colonisation of these species, the possibilities of overseas dispersal should not be ignored, considering the good dispersal abilities of some *Merodon* species. The analysis of between-island similarities in this study potentially indicates the importance of historical events for relationships of geographical variables with species numbers for *Merodon*. Such a case was shown previously (Fattorini,

2011) and could be interpreted with regard to interactions of historical and present factors, and their complex impact on current distribution of organisms on islands. Paleo-geographic and paleo-ecological events, along with present geographical and ecological features, affect existing distributional patterns (Fattorini, 2009).

Our cluster analysis results imply that there are two main tendencies regarding the similarities of the *Merodon* faunas on eastern Mediterranean islands (Fig. 3). The fauna of bigger islands is closely related to the adjacent mainland fauna, thus belonging to separate clusters in the dendrogram (Chios, Lesbos, Rhodes, Samos and Kos, close to the Anatolian mainland; and on the other hand Corfu, Peloponnese and Crete close to the Balkan Peninsula). These areas also harbour the highest *Merodon* species numbers. Lesbos has the highest number of *Merodon* species among the islands of the whole study area (25 species), while also Samos and Rhodes have high species numbers (Table S1), which fits well with the high number of species found in the adjacent mainland area (western Turkey with 34 recorded species). Peloponnese, Crete and Corfu also have high species numbers, in congruence with the high species diversity recorded from Central Greece (Table S1). Smaller islands form faunal similarity clusters consisting of geographically closely situated islands (such as Cyclades group and Euboea) or clusters of islands depending on nearest mainland (island cluster of Ithaca and Kefalonia close to the Balkan Peninsula; and cluster with Ikarria and Karpathos, near the Anatolian mainland).

There were two exceptions to these general trends. The first one being the classification of Syros and Delos, which are small islands in the middle of the Cyclades with small numbers of recorded *Merodon* species (three and one respectively). Both islands share *Merodon* aff. *albifasciatus* 2, a species with Anatolian origin, present on many other Cyclades islands, but without any species originating from Balkan Peninsula which is the closest mainland (Figs 1 and 3). It could be acknowledged that a clustering based on the Sørensen Similarity Index is not optimal for placing Syros and Delos, islands with a low species number, with other geographically proximate islands, but with different faunal compositions. The second exception is Samothraki, which is a somewhat larger island but with only three *Merodon* species recorded, as opposed to the higher *Merodon* species numbers found on some islands smaller than Samothraki (Table S1). The cluster analysis suggests it as an independent island, isolated from all others (Fig. 3). The island could be an example of an island previously rich in species, but presently harbouring only remnants of this fauna, reduced by extreme human influence such as domestic animal overgrazing and other land use considerably altering natural habitats (Theodora Petanidou pers. observ.). Analogous to Samothraki, Malta is an example of a larger island that was under intensive human impact for many centuries and presently only one *Merodon* species can be found on the island (FSUNS data, unpublished database).

Lastly, there are certainly other factors that can influence the richness of *Merodon* species, such as high habitat heterogeneity and diversity of certain host plant groups (geophytes) which have not been studied here. Further knowledge of feeding ecology of the immature stages of *Merodon* species, the migration abilities as well as resource and habitat requirements among particular species is undoubtedly needed, in order to make species-specific conclusions more comprehensive.

Additionally, the presence of 21 other *Merodon* species on the mainland areas (FSUNS data, unpublished database) surrounding the eastern Mediterranean islands with its 57 species, is a potential source of future colonisations and/or introductions. Thus, this study could be identified as an important platform on which future follow-up studies could be based.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12156:

Figure S1. Species accumulation curves as an indication of the sampling effort through plot of cumulative number of species versus collecting days for each island.

Table S1. Composition of *Merodon* fauna (by zoogeographical categories as in Table 1) and eco-geographical variables for eastern Mediterranean Islands. Numbers in zoogeographical categories rows indicate number of recorded species for each category per island. Numbers in species rows indicate number of collected specimens per island.

Table S2. Presence of different zoogeographical categories of *Merodon* species on eastern Mediterranean Islands (categories as in Table 1).

Table S3. Presence of four main zoogeographical categories of *Merodon* species on eastern Mediterranean Islands.

References

Báldi, A. & Kisbenedek, T. (1999) Orthopterans in small steppe patches: an investigation for the best-fit model of the species-area curve and evidences for their non-random distribution in the patches. *Acta Oecologica*, **20**, 125–132.

- Barton, K. (2015) MuMIn: Multi-Model Inference. R package version 1.15.1. <<http://CRAN.R-project.org/package=MuMIn>> 1st November 2015.
- Blondel, J.J., Aronson, J., Bodiou, J.-Y. & Boeuf, G. (2010) *The Mediterranean Region: Biological Diversity in Space and Time*. Oxford University Press, Oxford, UK.
- Cardoso, P., Borges, P.A.V., Carvalho, J.C., Rigal, F., Gabriel, R., Cascalho, J. & Correia, L. (2015) Automated discovery of relationships, models and principles in ecology. *bioRxiv* doi:10.1101/027839.
- Cardoso, P., Rigal, F. & Carvalho, J.C. (2015) BAT - Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, **6**, 232–236.
- Chatzaki, M., Thaler, K. & Mylonas, M. (2002) Ground spiders (Gnaphosidae; Araneae) of Crete (Greece). Taxonomy and distribution. I. *Revue suisse de Zoologie*, **109**, 559–602.
- Chatzimanolis, S., Trichas, A., Giokas, S. & Mylonas, M. (2003) Phylogenetic analysis and biogeography of Aegean taxa of the genus *Dendarus* (Coleoptera: Tenebrionidae). *Insect Systematics and Evolution*, **34**, 295–312.
- Connor, E.F. & McCoy, E.D. (1979) The Statistics and Biology of the Species-Area Relationship. *The American Naturalist*, **113**, 791–833.
- Dapporto, L. & Cini, A. (2007) Faunal patterns in Tuscan archipelago butterflies: the dominant influence is recent geography not paleogeography. *European Journal of Entomology*, **104**, 497–503.
- Dengler, J. (2009) Which function describes the species–area relationship best? A review and empirical evaluation. *Journal of Biogeography*, **36**, 728–744.
- Dennis, R.L.H., Shreeve, T., Olivier, A. & Coutsis, J.G. (2000) Contemporary geography dominates butterfly gradients within the Aegean archipelago (Lepidoptera: Papilionidea, Hesperioidea). *Journal of Biogeography*, **27**, 1365–1383.
- Dermitzakis, D.M. (1990) Paleogeography, geodynamic processes and event stratigraphy during the late cenozoic of the Aegean area. International Symposium: Biogeographical aspects of Insularity. Rome 18–22 May, 1987. Accad. Nat. dei Lincei, pp. 263–287.
- Dermitzakis, D.M. & Papanikolaou, D.J. (1981) Paleogeography and geodynamics of the Aegean region during the Neogene. *Annales Géologiques des Pays Helléniques*, **30**, 245–289.
- Dirickx, H.G. (1994) *Atlas des Diptères Syrphides de la Région Méditerranéenne*. L'Institut royal des sciences naturelles de Belgique, Bruxelles, Belgium.
- Fattorini, S. (2002) Biogeography of the tenebrionid beetles (Coleoptera, Tenebrionidae) on the Aegean Islands (Greece). *Journal of Biogeography*, **29**, 49–67.
- Fattorini, S. (2006) Spatial patterns of diversity in the tenebrionid beetles (Coleoptera, Tenebrionidae) of the Aegean Islands (Greece). *Evolutionary Ecology Research*, **8**, 237–263.
- Fattorini, S. (2009) Faunal patterns in tenebrionids (Coleoptera: Tenebrionidae) on the Tuscan Islands: the dominance of paleogeography over Recent geography. *European Journal of Entomology*, **106**, 415–423.
- Fattorini, S. (2011) Biogeography of tenebrionid beetles (Coleoptera: Tenebrionidae) in the circum-Sicilian islands (Italy, Sicily): multiple biogeographical patterns require multiple explanations. *European Journal of Entomology*, **108**, 659–672.
- Fox, J. & Weisberg, S. (2011) *An {R} Companion to Applied Regression*, Second Edition. Sage, Thousand Oaks, California.
- Gentile, G. & Argano, R. (2005) Island biogeography of the Mediterranean sea: the species–area relationship for terrestrial isopods. *Journal of Biogeography*, **32**, 1715–1726.
- Hausdorf, B. & Hennig, C. (2005) The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. *Biological Journal of the Linnean Society*, **84**, 785–795.
- Hurkmans, W. (1993) A monograph of *Merodon* (Diptera: Syrphidae) Part 1. *Tijdschrift voor Entomologie*, **136**, 147–234.
- Kelley, L.A., Gardner, S.P. & Sutcliffe, M.J. (1996) An automated approach for clustering an ensemble of NMR derived protein structures into conformationally-related subfamilies. *Protein Engineering*, **9**, 1063–1065.
- Kouli, K. (2012) Vegetation development and human activities in Attiki (SE Greece) during the last 5,000 years. *Vegetation History and Archaeobotany*, **21**, 267–278.
- Krijgsman, W., Hilgen, F.J., Raffi, I., Sierro, F.J. & Wilson, D.S. (1999) Chronology, causes and progression of the Messinian salinity crisis. *Nature*, **400**, 652–655.
- Lobo, J.M. & Martin-Piera, F. (1999) Between-group differences in the Iberian dung beetle species–area relationship (Coleoptera: Scarabaeidae). *Acta Oecologica*, **20**, 587–597.
- Lomolino, M.V., Riddle, B.R., Whittaker, R.J. & Brown, J.H. (2010) *Biogeography*. Sinauer Associates, Sunderland, Massachusetts.
- Losos, J.B. & Ricklefs, R.E. (2009) *The Theory of Island Biogeography Revisited*. Princeton University Press, Princeton, New Jersey.
- Losos, J.B. & Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature*, **408**, 847–850.
- Lymberakis, P. & Poulakakis, N. (2010) Three continents claiming an archipelago: the evolution of Aegean Herpetofaunal diversity. *Diversity*, **2**, 233–255.
- MacArthur, R. & Wilson, E. (1963) An Equilibrium Theory of Insular Zoogeography. *Evolution*, **17**, 373–387.
- MacArthur, R. & Wilson, E. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Muhlenberg, M., Leipold, D., Mader, H.J. & Steinhauer, B. (1977) Island ecology of arthropods. *Oecologia*, **29**, 117–134.
- Mylonas, M. (1982) *The Zoogeography and Ecology of the Terrestrial Mollusks of Cyclades*. Dissertation, University of Athens, Greece.
- Nielsen, A., Steffan-Dewenter, I., Westphal, C., Messinger, O., Potts, S.G., Roberts, S.P.M., Settele, J., Szentgyörgyi, H., Vaissière, B.E., Vaitis, M., Woyciechowski, M., Bazos, I., Biesmeijer, J.C., Bommarco, R., Kunin, W.E., Tscheulin, T., Lamborn, E. & Petanidou, T. (2011) Assessing bee species richness in two Mediterranean communities: importance of habitat types and appropriateness of sampling techniques. *Ecological Research*, **26**, 969–983.
- Nussbaum, R.A. (1984) Amphibians of the Seychelles. *Biogeography and Ecology of the Seychelles Islands*, pp. 379–415. (ed. by D.R. Stoddart), Junk, The Hague, The Netherlands.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2015) vegan: Community Ecology Package. R package version 2.3-1. <<http://CRAN.R-project.org/package=vegan>> 1st November 2015.
- Pérez-Bañón, C., Juan, A., Petanidou, T., Marcos-García, M.Á. & Crespo, M.B. (2003) The reproductive ecology of *Medicago citrina* (Font Quer) Greuter (Leguminosae), a bee-dependent plant in bee-deprived Mediterranean islands. *Plant Systematics and Evolution*, **241**, 29–46.

- Pérez-Bañón, C., Petanidou, T. & Marcos-García, M.Á. (2007) Pollination in small islands by occasional visitors: the case of *Daucus carota* subsp. *commutatus* (Apiaceae) in the Columbretes archipelago, Spain. *Plant Ecology*, **192**, 133–151.
- Perissoratis, C. & Conispoliatis, N. (2003) The impacts of sea-level changes during latest Pleistocene and Holocene times on the morphology of the Ionian and Aegean seas (SE Alpine Europe). *Marine Geology*, **196**, 145–156.
- Petanidou, T., Vujić, A. & Ellis, W.N. (2011) Hoverfly diversity (Diptera: Syrphidae) in a Mediterranean scrub community, Athens, Greece. *Annales de la Société Entomologique de France*, **47**, 168–175.
- Popov, G.V. (2001) *What and Where Are Merodon feeding?* First International Workshop on the Syrphidae. Staatliches Museum für Naturkunde, Stuttgart, Germany.
- Potts, S.G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A. & Willmer, P. (2006) Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. *Biological Conservation*, **129**, 519–529.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Radenković, S., Vujić, A., Ståhls, G., Pérez-Bañón, C., Petanidou, T. & Šimić, S. (2011) Three new cryptic species of the genus *Merodon* Meigen (Diptera: Syrphidae) from the island of Lesbos (Greece). *Zootaxa*, **2735**, 35–56.
- Ricarte, A., Marcos-García, M.Á. & Rotheray, G.E. (2008) The early stages and life histories of three *Eumerus* and two *Merodon* species (Diptera: Syrphidae) from the Mediterranean region. *Entomologica Fennica*, **19**, 129–141.
- Schmidt, M. & Lipson, H. (2015) Eureka (Version 1.24.0). <http://www.eureka.com/> 1st November 2015.
- Sfenthourakis, S. (1996a) A biogeographic analysis of terrestrial isopods (Isopoda, Oniscidea) from central Aegean islands (Greece). *Journal of Biogeography*, **23**, 687–698.
- Sfenthourakis, S. (1996b) The species–area relationship of terrestrial isopods (Isopoda; Oniscidea) from the Aegean Archipelago (Greece): a comparative study. *Global Ecology & Biogeography Letters*, **5**, 149–157.
- Sfenthourakis, S. & Giokas, S. (1998) A biogeographic analysis of Greek Oniscidean endemism. *Israel Journal of Zoology, Special Issue: Proceedings: Fourth Symposium on the Biology of Terrestrial Isopods*, **44**, 273–282.
- Simaiakis, S., Minelli, A. & Mylonas, M. (2005) The centipede fauna (Chilopoda) of the south Aegean archipelago (Greece, eastern Mediterranean). *Israel Journal of Zoology*, **51**, 241–307.
- Simaiakis, S.M., Tjørve, E., Gentile, G., Minelli, A. & Mylonas, M. (2012) The species–area relationship in centipedes (Myriapoda: Chilopoda): a comparison between Mediterranean island groups. *Biological Journal of the Linnean Society*, **105**, 146–159.
- Sondaar, P.Y. & van der Geer, A.A.E. (2002) Plio-Pleistocene terrestrial vertebrate faunal evolution on Mediterranean islands, compared to that of the Palearctic mainland. *Annales Géologiques des Pays Helléniques*, **39**, 165–180.
- Speight, M.C.D. (2013) Species accounts of European Syrphidae (Diptera). *Syrph the Net, the database of European Syrphidae*, Syrph the Net publications, Dublin, Ireland.
- Ståhls, G., Vujić, A., Pérez-Bañón, C., Radenković, S., Rojo, S. & Petanidou, T. (2009) COI barcodes for identification of *Merodon* hoverflies (Diptera, Syrphidae) of Lesbos Island, Greece. *Molecular Ecology Resources*, **9**, 1431–1438.
- Stathi, I. & Mylonas, M. (2000) The Scolopendra species (Chilopoda: Scolopendromorpha: Scolopendridae) of Greece (E-Mediterranean): a theoretical approach on the effect of geography and palaeogeography on their distribution. *Zootaxa*, **1792**, 39–53.
- Steinbauer, M.J., Irl, S. & Beierkuhnlein, C. (2013) Elevation driven ecological isolation promotes diversification on Mediterranean islands. *Acta Oecologica*, **47**, 52–56.
- Strid, A. (1970) Studies in the Aegean Flora. XVI. Biosystematics of the *Nigella arvensis* complex with special reference to the problem of non-adaptive radiation. *Opera Botanica*, **28**, 1–169.
- Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species–area relationship: biology and statistics. *Journal of Biogeography*, **39**, 215–231.
- Triantis, K.A. & Mylonas, M. (2009) Greek islands, biology. *Encyclopedia of Islands* (ed. by R. Gillespie and D.A. Glague), University of California Press, Berkeley, California.
- Triantis, K.A., Sfenthourakis, S. & Mylonas, M. (2008) Biodiversity patterns of terrestrial isopods from two island groups in the Aegean Sea (Greece): species–area relationship, small island effect, and nestedness. *Écoscience*, **15**, 169–181.
- Trichas, A. & Legakis, A. (1987) General considerations on the distribution of Coleoptera in the Aegean islands. *Biologia Gallo-Hellenica*, **13**, 127–132.
- Vardinoyannis, K. (1994) *Biogeography of Land Snails in the South Aegean Island Arc*. Dissertation, University of Athens, Greece.
- Vujić, A., Pérez-Bañón, C., Radenković, S., Ståhls, G., Rojo, S., Petanidou, T. & Šimić, S. (2007) Two new species of genus *Merodon* Meigen, 1803 (Syrphidae, Diptera) from the island of Lesbos (Greece), in the eastern Mediterranean. *Annales de la Société entomologique de France*, **43**, 319–326.
- Vujić, A., Radenković, S., Likov, L., Trifunov, S. & Nikolić, T. (2013) Three new species of the *Merodon nigritarsis* group (Diptera: Syrphidae) from the Middle East. *Zootaxa*, **3640**, 442–464.
- Vujić, A., Radenković, S., Ståhls, G., Ačanski, J., Stefanović, A., Veselić, S., Andrić, A. & Hayat, R. (2012) Systematics and taxonomy of the *ruficornis* group of genus *Merodon* Meigen (Diptera: Syrphidae). *Systematic Entomology*, **37**, 578–602.
- Welter-Schultes, F.W. & Williams, M.R. (1999) History, island area and habitat availability determine land snail species richness of Aegean islands. *Journal of Biogeography*, **26**, 239–249.
- White, D. & Gramacy, R.B. (2012) maptree: Mapping, pruning, and graphing tree models. R package version 1.4-7. <http://CRAN.R-project.org/package=maptree> 1st November 2015.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island Biogeography: Ecology, Evolution, and Conservation*, 2nd edn. Oxford University Press, Oxford, UK.

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