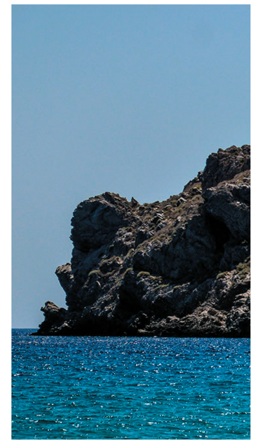

The Zoogeographic Regions of the Aegean Sea: A Multi-Taxon Approach

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ABSTRACT

The Aegean archipelago is a typical archipelago of continental islands which stands at the crossroads of Europe, Asia and Africa. Herein we present one of the few global studies of bioregionalization,i.e., the process of identifying, delimiting and naming biogeographical regions, based on eight animal taxa, namely ants (Formicidae), land birds, reptiles and amphibians, land snails, terrestrial isopods (Oniscidea), tenebrionid beetles (Tenebrionidae), Lepidoptera, Orthoptera and centipedes (Chilopoda). Dispersal ability, ecological requirements, and endemism seem to shape the major biogeographical regions identified. Further insights on the processes establishing biodiversity patterns can be gained by such multi-taxon approaches.

INTRODUCTION

Already in the 19th century, naturalists such as von Humboldt and Bonpland (1807), Sclater (1858) and Wallace (1876) had noticed that the globe's biota can be divided into a number of more or less distinct geographical units. Wallace (1876) used existing knowledge of his time on the distribution and taxonomic relationships of vertebrate families (Sclater, 1858), and divided the world into six terrestrial zoogeographic units and further recognised four subregions in each major unit. His was the first map of global terrestrial zoogeographic regions (see Holt et al., 2013). The identification of biogeographical regions (geographically distinct assemblages of species and communities) is a critical step towards unveiling processes establishing species diversity and understanding the origins and relationships between distinct faunal/floristic assemblages (e.g. Kreft & Jetz, 2010; Holt et al., 2013; Vilhena & Antonelli, 2015; Ficetola, Mazel, & Thuiller, 2017). The development and integration of several multivariate hierarchical and network approaches (e.g., Kreft & Jetz, 2010; Leprieur & Oikonomou, 2014; Vilhena & Antonelli, 2015; Edler, Guedes, Zizka, Rosvall, & Antonelli, 2017; Ficetola et al., 2017), in conjunction with the increasing availability of species distribution data, has sparkled a new interest in biogeographical research at continental and global scales (Kreft & Jetz, 2010; Holt et al., 2013; Ficetola et al., 2017) but also at local ones (Carstensen et al., 2012; Kougioumoutzis, Simaiakis, & Tiniakou, 2014; Oikonomou, Leprieur, Leonardos, 2014; Kougioumoutzis et al., 2017).

Islands have been the focal research area for several biogeographical phenomena and island research has culminated in the development of essential contributions to our understanding of key ecological and evolutionary processes (e.g., immigration, extinction, turnover, speciation, taxon cycles) and biodiversity patterns. Islands constitute ideal study systems due to their comparatively small size, distinct boundaries and, usually, less complex biota (Whittaker & Fernández-Palacios, 2007; Whittaker, Fernández-Palacios, Matthews, Borregaard, & Triantis, 2017). Today, the focus on island research is stronger than ever (Warren et al., 2015) even though insular faunas are considered species-poor and being on the receiver's end of the colonization process (e.g. MacArthur & Wilson, 1967; but see Bellemain & Ricklefs, 2008). In this context, oceanic islands and archipelagos have drawn much more attention compared to continental island systems (e.g., Whittaker, Triantis, & Ladle, 2008; Triantis, Economo, Guilhaumon, & Ricklefs, 2015; Triantis, Whittaker, Fernández-Palacios, & Geist, 2016; Borregaard et al., 2017; Whittaker et al., 2017).

However, the vast majority of true geographical islands are not oceanic but continental-shelf islands. Considering only those with an area larger than 1 km^2, they represent a 27% of the total number of islands worldwide (Weigelt, Jetz, & Kreft, 2013). Although an accurate estimation of all the geographical islands of the world is not available, oceanic islands represent an even smaller fraction according to the crude estimation of ca. 1 million islands in the globe by Fernández-Palacios (2011).

The Aegean Sea hosts a typical archipelago of continental-shelf islands that has long fascinated biogeographers (e.g., Rechinger, 1943; Rechinger & Rechinger-Moser, 1951; Wettstein, 1953; Runemark, 1970, 1971; Greuter, 1975; Mylonas, 1982, 1984; Sfenthourakis, 1996a,b; Strid, 1996, 2016; Sfenthourakis, Giokas, & Mylonas, 1999; Fattorini, 2002; Hausdorf & Hennig, 2005; Simaiakis, Minelli & Mylonas, 2005; Comes, Tribsch, & Bittkau, 2008; Bittkau & Comes, 2009; Papadopoulou et al., 2011; Triantis & Sfenthourakis, 2012; Simaiakis et al., 2012, 2017; Kougioumoutzis et al., 2014, 2017; Poulakakis et al., 2015; Sfenthourakis & Triantis, 2017; Jaros, Tribsch, & Comes, 2017), since it constitutes one of the largest archipelagos in the world, with more than 7,000 islands and islets lying at the crossroads of three different biogeographical regions, namely Europe, Asia and Africa (Triantis & Mylonas, 2009; Sfenthourakis & Triantis, 2017). Its high environmental and topographical heterogeneity, complex palaeogeographical history, as well as high diversity and endemism, render it an ideal stage for biodiversity and biogeographical studies (Triantis & Mylonas, 2009; Trigas, Panitsa, & Tsiftsis, 2013; Sfenthourakis & Triantis, 2017). Recently, based on the distribution of 1,498 plants from 59 islands, Kougioumoutzis et al. (2017) identified six different biogeographical areas for plants, which correspond well to the Aegean's palaeogeography from the middle Miocene to the end of the Pleistocene (Figure 1). However, a similar approach for animals is still missing.

Herein we present the first study on bioregionalization (the process of identifying, delimiting and naming biogeographical regions) of the

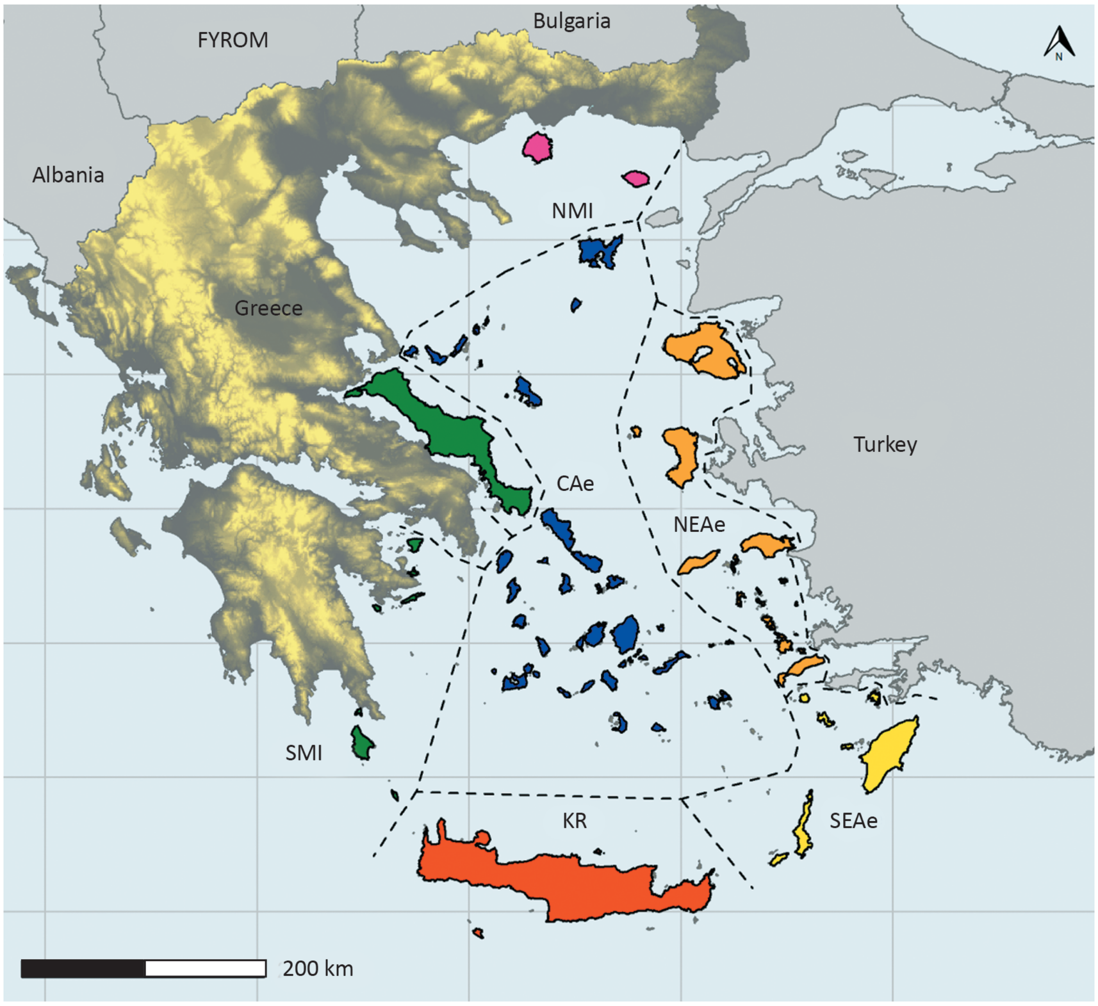

FIGURE 1 ■ The major phytogeographical regions of the Aegean Sea based on Kougioumoutzis et al. (2017). Green: South Mainland & Islands, Fuchsia: North Mainland & Islands, Orange: North-Eastern Aegean, Blue: Central Aegean, Red: Crete, Yellow: South-Eastern Aegean.

Aegean Sea based on several animal taxa. This is amongst the few global studies incorporating data from multiple taxa, both vertebrates and invertebrates, encompassing a variety of ecological requirements and evolutionary histories.

THE MAJOR PALAEOGEOGRAPHICAL BARRIERS OF THE AEGEAN SEA

The palaeogeography of the Aegean has largely shaped current biodiversity patterns (Greuter, 1975; Mylonas, 1982, 1984; Sfenthourakis, 1996a; Comes et al., 2008; Triantis & Mylonas, 2009; Lymberakis & Poulakakis, 2010; Poulakakis et al., 2015; Kougioumoutzis et al., 2017; Sfenthourakis & Triantis, 2017). Three main distributional and palaeogeographical barriers reign supreme in the Aegean archipelago (Figure 2, see the review by Poulakakis et al., 2015; Sakellariou & Galanidou, 2016; Sakellariou et al., 2017; and Fassoulas, present volume): (1) the formation of the Mid-Aegean Trench (MAT), (2) the isolation of Crete from Peloponnisos after the Messinian Salinity Crisis, and (3) the separation of Kasos and Karpathos from Rodos in the Pliocene. Most important in terms of geographical and temporal extent is the formation of a sea barrier (the MAT), which initiated at the end of middle Miocene (12 Ma) and was fully completed in the late Miocene (10–9 Ma). The opening of the MAT started with sea intrusion separating Crete from the Karpathos' is-

FIGURE 2 ■ The major geological barriers in the Aegean Sea, based on Lymberakis & Poulakakis (2010) (see also Poulakakis et al., 2015) (numbers in millions of years).

land complex at 12 Mya. This initial split then bifurcated, forming the N–S axis of the MAT that reached up to the modern island of Thasos (9 Ma) and separated the Cyclades from the East Aegean islands (both parts of continental masses at the time), and a second westward split (10–9 Mya) that separated the Cyclades from Crete and Peloponnisos (Dermitzakis, 1990; Sakellariou et al., 2017). It is reasonable to expect a strong signal of these splits in the composition of modern biota. In addition, we should also stress the fact that most eastern Aegean islands have been isolated from Asian mainland very recently, in effect only a few thousand years ago after the last glacial period. Therefore, relaxation processes should have been in action on several of these islands, variably affecting biotic composition (see Triantis, Sfenthourakis, & Mylonas, 2008). Of course, environmental factors too, such as temperature and precipitation gradients, might have played a role in shaping insular biota in the Aegean.

METHODS

Sources of data

We recorded the distribution of nine major animal taxa, i.e. ants (Formicidae), land birds (breeding), reptiles and amphibians (hereafter herptiles), land snails, terrestrial isopods (Oniscidea), tenebrionid beetles (Tenebrionidae), Lepidoptera, Orthoptera and centipedes (Chilopoda) on a total of 64 islands of the Aegean Sea (Table 1). Only islands larger than 9 km^2 were considered. In addition to published records, we also used unpublished information from the authors and museum collections to compile the most updated lists of native species for all taxa. The number of islands for each taxon varied from 29 for isopods to 64 for herptiles.

Delimiting bioregions with networks

The biogeographical delimitation within archipelagos involves species distributions across an island system that can be treated as an island-

Table 1 ■ The Aegean islands considered in this work, their area.

Island	Area	Island	Area
Crete	8264.6	Serifos	74.1
Evvoia	3654.5	Kasos	66.7
Lesvos	1636.7	Alonnisos	64.1
Rodos	1407.7	Tilos	61,8
Chios	842.0	Symi	58.0
Samos	477.4	Leros	54.4
Limnos	477.0	Idra	49.8
Naxos	430.2	Skiathos	47.3
Thasos	383.7	Agios Efstratios	42.0
Andros	381.0	Sikinos	41.7
Karpathos	300.9	Nisyros	41.3
Kos	288.1	Psara	40.0
Kythira	277.2	Anafi	38.5
Ikaria	254.7	Kimolos	37.3
Skyros	206.9	Antiparos	35.1
Paros	196.3	Patmos	34.2
Tinos	194.5	Gavdos	32.7
Samothraki	180.5	Folegandros	32.4
Milos	158.3	Fournoi	30.6
Kea	130.4	Chalki	27.2
Amorgos	121.3	Kyra Panagia	24.8
Kalymnos	110.8	Poros	22.9
Ios	108.4	Spetses	20.6
Kythnos	99.4	Saria	20.5
Astypalaia	95.9	Antikythira	19.7
Salamina	95.4	Irakleia	18.1
Skopelos	95.1	Polyaigos	18.1
Mykonos	85.8	Elafonisos	18.0
Aegina	84.2	Gyaros	17.6
Syros	83.8	Leipsoi	15.9
Sifnos	77.4	Pserimos	14.6
Santorini	75.7	Kastelorizo	9.11

species network. Islands may differ regarding their role in connecting the biotas across an archipelago. Differences in geophysical characteristics, geological origin, spatial arrangement within the archipelago, and the palaeogeographical evolution of each respective island determineits biogeographical role. In this context, network biogeographical analysis based on species distributions, that provides a comprehensive approach, free of *a priori* dataset assumptions (Dos Santos, Fernandez, Cuezzo, & Dominguez, 2008), is a powerful tool for detecting both coarse- and fine-grained biogeographical patterns, as it accurately depicts the biogeographical structure of datasets regardless their size (e.g. Carstensen et al., 2012; Kougioumoutzis et al., 2014, 2017; Bloomfield, Knerr, & Encinas-Viso, 2017).

NETCARTO (Guimerá & Amaral, 2005a) is a module-detecting algorithm used, *inter alia*, in ecological (Olesen, Bascompte, Dupont, & Jordano, 2007) and biogeographical studies (Carstensen et al., 2012). NETCARTO detects fine-grained biogeographical patterns (Carstensen & Olesen, 2009) and identifies the spatial importance of islands beyond that based on species richness patterns.

On the other hand, hierarchical clustering techniques have been widely used at continental and global scales in the definition of biogeographical regions by quantifying the spatial turnover and composition of species between sites (e.g., Kreft & Jetz, 2010; Oikonomou et al., 2014; He, Kreft, Gao, Wang, & Jiang, 2017). We applied hierarchical clustering too, but results were less informative from a biogeographical point of view, therefore we only discuss results from the network approach.

The bipartite island–taxa networks were constructed from the presence/absence matrices. We used NETCARTO, which uses an algorithm based on simulated annealing in order to assign all nodes (taxa and islands) to modules (Guimerá & Amaral, 2005a,b). NETCARTO also provides the empirical network's significance level of M by comparing its value to that of 100 random networks with the same linkage level as the empirical one. A node's linkage level is the number of links it has to other nodes. If the empirical M value lies above the 95% confidence interval for *M* in the randomized networks, the empirical network is significantly modular.

This analysis was carried out in R 3.3.2 (R Development Core Team, 2016), using functions from the 'igraph' (Csárdi & Nepusz, 2006) and 'rnetcarto' (Doulcier & Stouffer, 2015) packages. The networks were visualized with GEPHI 0.9.2 beta (Bastian, Heymann, & Jacomy, 2009) using the force-based algorithm FORCE-ATLAS (Jacomy, 2009).

RESULTS & DISCUSSION

To our knowledge, this is the first study that focuses on the compartmentalization and biogeography of a highly diverse, non-oceanic archipelago, that of the Aegean Sea, taking into account eight animal higher taxa. The biogeographical regions recognised differ among taxa (Table 2; Figures 3-11). However, despite the varying ecologies and evolutionary histories of the studied taxa, the varying number of islands considered for each taxon (Table 2), and the different quality of distributional and taxonomical data among taxa, some general patterns can still be detected.

a) For vertebrate taxa, birds and herptiles, the modules identified show no relevance to current geography or palaeogeography (Figures 5 and 10). Distant islands are grouped together and this can be attributed to the fact that both taxa have many widespread species, whose presence depends on factors such as climate, vegetation and human impacts, with palaeogeography playing a secondary role. The importance of annual precipitation for reptile community composition of central Aegean islands has been stressed also by Hausdorf and Hennig (2005). Regarding birds, the fact that there is no single endemic species in the Aegean is indicative of the important role played by the taxon's dispersal abilities in shaping biogeographical patterns.

b) In the majority of cases Crete appears as a distinct biogeographical region or acts as a network hub island, i.e. an island important to the coherence of the network (Carstensen & Olesen, 2009; Carstensen et al., 2012). In the Messinian (upper Miocene), Crete was isolated from the rest of the Aegean region by extensive saline deserts and/or saline/hypersaline lakes (Poulakakis et al., 2015). After the end of the Messinian the island never reconnected to the mainland, even though it went through extensive topographical changes (e.g., in the Pliocene, large parts of Crete were submerged). As a result of a ca. 5 My -long isolation, Crete hosts a high percentage of endemic species for almost all taxa considered herein (see respective chapters in this volume).

c) Crete and Karpathos, despite their geographical proximity, are not grouped together for any taxon. This is indicative of the strong ef-

Table 2 ■ Taxa considered, the number of islands for which data existed for each taxon, and the number of biogeographical regions.

Taxon	Number of islands	Number of species	Number of biogeographical regions
Land birds	53	101	3
Reptiles and amphibians	64	66	4
Land snails	42	386	5
Terrestrial isopods (Oniscidea)	29	83	4
Ants (Formicidae)	48	195	7
Lepidoptera	56	1613	5
Orthoptera	45	135	5
Coleoptera (Tenebrionidae)	40	204	5
Chilopoda	42	70	5

fect of the MAT on current biotic affinities, especially in the south where it started forming (Figure 2). This finding is in concordance with results for Aegean plants (Kougioumoutzis et al. 2017; Figure 1).

d) Cyclades are not always identified as a distinct biogeographical unit. They form a continental-shelf island group off the eastern coast of mainland Greece, segregated from eastern Aegean islands. During the Last Glacial Maximum, approximately 60 islands were merged into the 'Mega-Cyclades palaeo-island', which was fragmented back to an archipelago during the subsequent sea level rise by the end of the Ice Age. Cyclades since their original isolation were reconnected to the mainland during lower sea-level stands (see Kapsimalis et al., 2009; Sakellariou & Galanidou, 2016; Sakellariou et al., 2017). The observation that Cyclades are not always appearing as a distinct biogeographical unit, indicates that the MAT, although a critical barrier for the biogeography of the Aegean Sea, it is not always dominant, especially for the central and northern parts of the archipelago (see also Poulakakis et al., 2015; Kougioumoutzis et al., 2017).

e) It appears that the less dispersive the taxa are the more important geography and palaeogeography are becoming in shaping species distribution patterns, thus biogeographical affinities. For land snails (Figure 11), for example, the biogeographical units are largely representative of the region's geological evolution when, on the other hand, birds and herptiles (Figures 3 and 10), show no such correlation. Hausdorf and Hennig (2005), using a different approach based on structural equations and partial Mantel tests for faunal distances and a variety of environmental, geographical and palaeogegraphical parameters, found a strong signal of recent and Pliocene distances of central Aegean islands on land snail, and terrestrial isopod communities, but also of recent and Miocene distances for butterflies (tenebrionid beetles did not show any relationship to the predictors used, but the dataset available at the time was far from complete). Of course, these authors focused on a subset of the islands included in the present analysis, so the discrepancy regarding the highly dispersive butterflies might be a result of scale-dependent patterns plus the different approach followed.

The idea that organismal distributions in the Aegean Sea often mirror palaeogeographical patterns (Mylonas, 1982) has received considerable support over the last years, particularly from phylogenetic, phylogeographical and population genetic studies on animals (reviewed in Poulakakis et al., 2015; see also Jaros et al. 2017; Sfenthourakis & Triantis, 2017). Results herein also concur to the importance of palaeogeography but at the same time, call for caution, since patterns should be seen under the prism of the particular ecological features and the variable evolutionary processes undergone by each taxon.

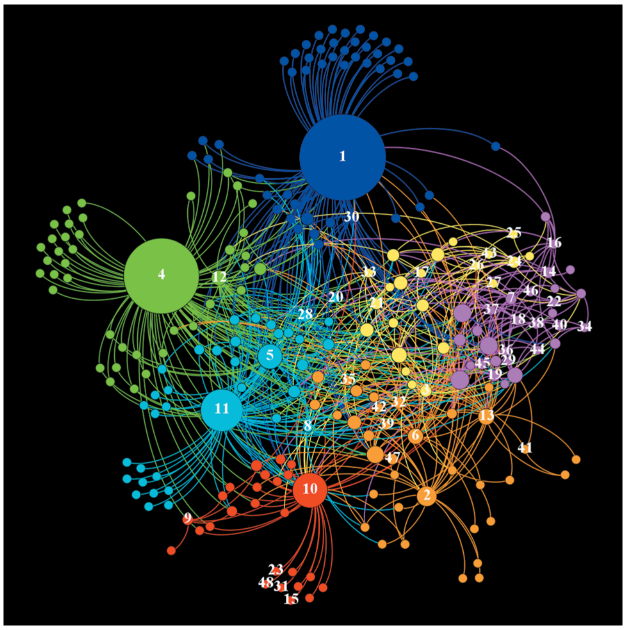

FIGURE 3 ■ Biogeographical modules of the Aegean Archipelago based on ants(Formicidae). **Module 1 (Blue):** Crete, Kasos. **Module 2 (Pink):** Anafi, Antiparos, Folegandros, Ios, Irakleia, Kea, Kimolos, Limnos, Makronissos, Milos, Paros, Serifos, Sikinos, Skyros, Spetses, Tinos. **Module 3 (Orange):** Chalki, Evvoia, Fournoi, Ikaria, Nisyros, Patmos, Pserimos, Samos, Symi. **Module 4 (Red):** Andros, Thasos. **Module 5 (Cyan):** Amorgos, Chios, Karpathos, Naxos, Santorini, Tilos. **Module 6 (Green):** Kastelorizo, Kos, Rodos. **Module 7 (Yellow):** Aigina, Kalymnos, Kyra Panagia, Kythnos, Lesvos, Mykonos, Samothraki, Skiathos, Skopelos, Syros.

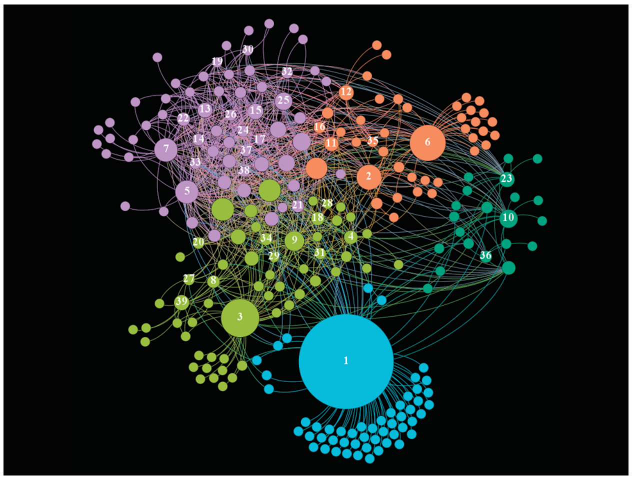

FIGURE 4 ■ Biogeographical modules of the Aegean Archipelago based on tenebrionid beetles. **Module 1 (Olive green):** Kalymnos, Karpathos, Kasos, Kastelorizo, Kos, Kythnos, Leros, Nisyros, Patmos, Rodos, Samos, Tilos. **Module 2 (Green):** Antikythira, Kythira, Syros. **Module 3 (Orange):** Folegandros, Ikaria, Kea, Lesvos, Skyros, Thasos. **Module 4 (Cyan)**: Crete. **Module 5 (Pink):** Amorgos, Anafi, Andros, Antiparos, Astypalaia, Donousa, Ios, Irakleia, Milos, Mykonos, Naxos, Paros, Santorini, Serifos, Sifnos, Sikinos, Tinos.

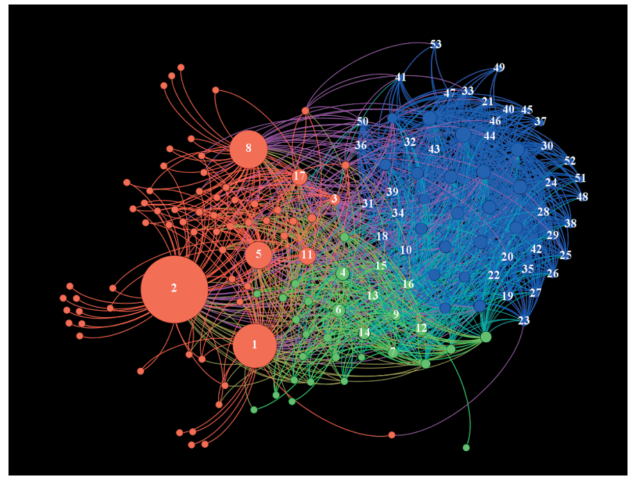

FIGURE 5 ■ Biogeographical modules of the Aegean Archipelago based on land birds. **Module 1 (Blue):** Agios Efstratios, Amorgos, Anafi, Antikythira, Antiparos, Astypalaia, Chalki, Dia, Donousa, Folegandros, Fournoi, Gavdos, Gyaros Irakleia, Ios, Kalymnos, Karpathos, Kasos, Kea, Keros, Kythnos, Leipsoi, Leros, Milos, Mykonos, Nisyros, Patmos, Polyaigos, Psara, Santorini, Saria, Serifos, Sifnos, Sikinos, Symi, Syros, Tilos. **Module 2 (Green):** Andros, Chios, Ikaria, Kythira, Limnos, Naxos, Paros, Skyros, Tinos. **Module 3 (Red):** Crete, Kos, Lesvos, Rodos, Samos, Samothraki, Thasos.

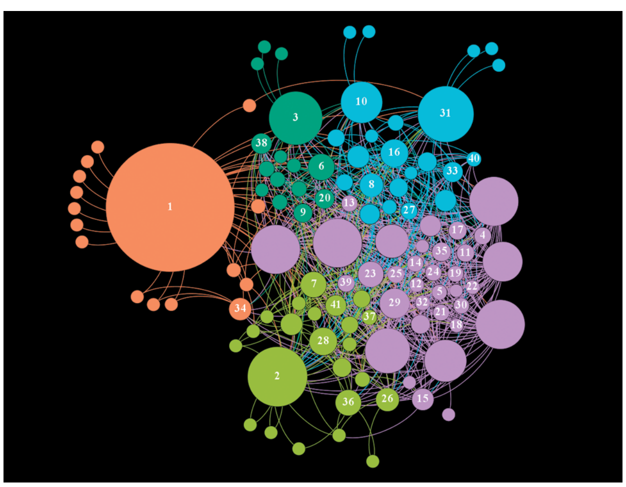

FIGURE 6 ■ Biogeographical modules of the Aegean Archipelago based on Chilopoda. **Module 1 (Orange):** Crete, Gavdos. **Module 2 (Pink):** Amorgos, Anafi, Astypalaea, Folegandros, Ios, Kea, Kythnos, Leipsoi, Leros, Limnos, Milos, Mykonos, Naxos, Paros, Santorini, Serifos, Sifnos, Sikinos, Syros, Tinos. **Module 3 (Green):** Andros, Antikythira, Chios, Kythira, Salamina. **Module 4 (Olive green):** Chalki, Karpathos, Kasos, Kastelorizo, Rodos, Saria, Symi. **Module 5 (Cyan):** Kalymnos, Kos, Nisyros, Patmos, Pserimos, Skyros, Tilos.

FIGURE 7 ■ Biogeographical modules of the Aegean Archipelago based on terrestrial isopods (Oniscidea). **Module 1 (Green):** Kalymnos, Kos, Leros, Nisyros, Patmos, Pserimos, Samos, Saria. **Module 2 (Blue):** Anafi, Andros, Antiparos, Dia, Kea, Kythnos, Mykonos, Paros, Serifos, Sifnos, Syros, Tinos. **Module 3(Cyan):** Antikythira, Crete, Kasos, Milos, Santorini. **Module 4 (Red):** Amorgos, Astypalaia, Ikaria, Naxos.

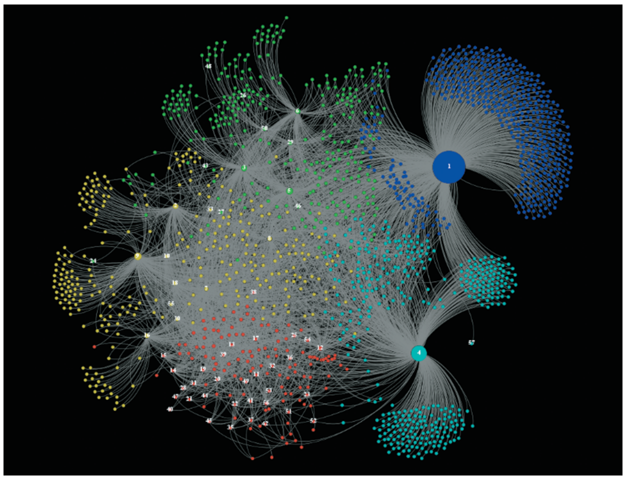

FIGURE 8 ■ Biogeographical modules of the Aegean Archipelago based on Lepidoptera. **Module 1 (Blue):** Crete. **Module 2 (Red):** Agios Efstratios, Amorgos, Antiparos, Astypalaia, Fournoi, Idra, Ikaria, Ios, Kalymnos, Karpathos, Kastelorizo, Kea, Kos, Kyra Panagia, Kythira, Leros, Makronisos, Milos, Mykonos, Nisyros, Paros, Patmos, Polyaigos, Psara, Pserimos, Santorini, Sifnos, Skiathos, Skyros, Spetses, Symi, Tilos. **Module 3 (Cyan):** Rodos, Antimilos. **Module 4 (Yellow):** Agkistri, Andros, Evvoia, Limnos, Naxos, Samothraki, Serifos, Syros, Thasos, Tinos. **Module 5 (Green):** Aegina, Anafi, Chalki, Chios, Folegandros, Kythnos, Lesvos, Poros, Salamina, Samos, Skopelos.

FIGURE 9 ■ Biogeographical modules of the Aegean Archipelago based on Orthoptera. **Module 1 (Olive green):** Chalki, Fournoi, Kalymnos, Karpathos, Kasos, Kos, Rodos. **Module 2 (Orange):** Chios, Lesvos, Nisyros, Psara, Samos, Symi. **Module 3 (Green):** Agios Efstratios, Limnos, Samothraki, Thasos. **Module 4 (Pink):** Amorgos, Anafi, Andros, Antiparos, Astypalaia, Folegandros, Ikaria, Ios, Kea, Kythnos, Mykonos, Milos, Naxos, Paros, Polyaigos, Santorini, Serifos, Sifnos, Sikinos, Skiathos, Skopelos, Skyros, Syros, Tinos. **Module 5 (Cyan):** Dia, Kimolos, Crete, Patmos.

FIGURE 10 ■ Biogeographical modules of the Aegean Archipelago based on reptiles and amphibians. **Module 1 (Pink):** Alonissos, Amorgos, Anafi, Antiparos, Antikythira, Astypalaia, Folegandros, Gavdos, Gyaros, Gioura, Idra, Ios, Irakleia, Karpathos, Kasos, Keros, Kyra Panagia, Mykonos, Naxos, Santorini, Saria, Sikinos, Skiathos, Skopelos. **Module 2 (Orange):** Chalki, Chios, Fournoi, Ikaria, Kalymnos, Kastelorizo, Leros, Nisyros, Patmos, Psara, Pserimos, Rodos, Symi, Tilos. **Module 3 (Green):** Aegina, Andros, Elafonisos, Kea, Kimolos, Kythira, Kythnos, Crete, Milos, Paros, Polyaigos, Serifos, Sifnos, Syros, Skyros, Spetses, Tinos. **Module 4 (Cyan)**: Agios Efstratios, Evvoia, Kos, Lesvos, Limnos, Salamina, Samos, Samothraki, Thasos.

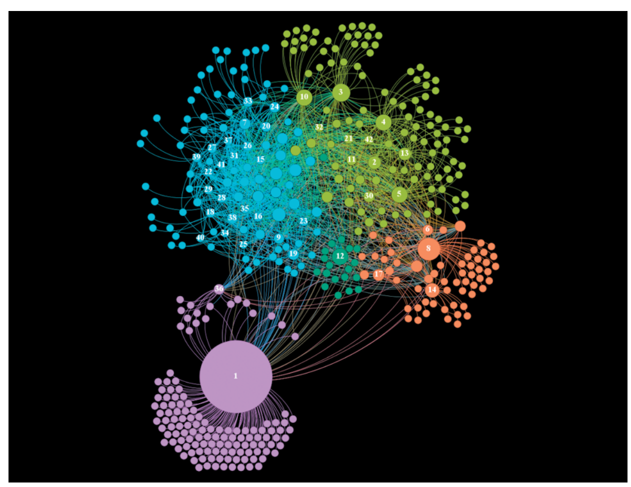

FIGURE 11 ■ Biogeographical modules of the Aegean Archipelago based on land snails. **Module 1 (Cyan):** Amorgos, Anafi, Andros, Antikythira, Antiparos, Astypalaia, Folegandros, Gyaros, Ios, Irakleia, Kea, Kimolos, Kythnos, Milos, Mykonos, Naxos, Paros, Polyaigos, Santorini, Serifos, Sifnos, Sikinos, Syros, Tinos. **Module 2 (Green):** Kythira. **Module 3 (Olive green):** Chios, Ikaria, Kalymnos, Karpathos, Kos, Leros, Lesvos, Nisyros, Pserimos, Rodos, Samos. **Module 4 (Orange):** Limnos, Samothraki, Skyros, Thasos. **Module 5 (Pink):** Crete, Gavdos.

Potential caveats

Our study has several limitations. First, we did not use the exact same set of islands for all taxa considered. Second, we consider all native species, not only Aegean or Greek endemics that might be more informative (see Kougioumoutzis et al., 2017). Especially for widespread taxa, such as Lepidoptera, the inclusion of all native species might veil the effect of major biogeographical barriers, lowering thus the distinctiveness among regions. Third, although we considered the most up-to-date distributional data for each taxon, some taxa are less well-known compared to others, with some islands or island groups not having been adequately sampled (e.g. Triantis, Vardinoyannis, & Mylonas, 2008). Fourth, the animal groups considered are not taxonomically equivalent, since some groups represent Orders (e.g., Lepidoptera), others are sub-Orders (e.g., Oniscidea) or Families (e.g., Tenebrionidae), while Chilopoda, reptiles and amphibians consist Classes. Finally, the potential effect of island size, therefore species richness, has not been addressed. Smaller islands, with on average poorer biotas, might affect the overall outcome.

Future steps

A more focused future study should: a) evaluate the completeness of data at both the distributional and the taxonomic levels, b) consider the potential effects of parameters such as current and past climate, vegetation and geologic processes (e.g., Ficetola et al., 2017; He et al., 2017), especially sea-level fluctuations (see Simaiakis et al., 2017), c) focus on Greek, mainly Aegean endemics, reducing thus the effects of widespread taxa, d) consider only those islands for which information for all taxa is available, and finally, e) consider all taxa together, using some kind of weighing to reduce effects of differential species richness among taxa.

The most challenging task in unveiling biogeographical relationships across the Aegean Sea archipelago rests upon the long and intensive human influence. Modern humans are continuously present on the majority of the larger Aegean islands for more than 10,000 years, shaping not only their insular environment and habitats but also their biotas through local extirpations, introduction of exotic and invasive species, and by the transfer of species, intentionally and unintentionally, across islands (see discussion in Sfenthourakis & Triantis, 2017). Mylonas (1984) identified early on what is now known as the island biogeography of the Anthropocene (e.g. Helmus, Mahler, & Losos, 2014; Whittaker et al., 2017), i.e. how human activities are shaping long-standing biogeographical patterns. He did so by highlighting the effect synanthropic and anthropochorous but still indigenous species have. Before even the term Anthropocene was popularized, Mylonas, provided evidence that, unlike island biogeography of the past, in the Anthropocene island biogeography is mainly dominated by the presence and activities of human populations (cf. Helmus et al., 2014).

REFERENCES

Bastian, M., Heymann, S., & Jacomy, M. (2009). *Gephi: An open source software for exploring and manipulating networks.* International AAAI Conference on Weblogs and Social Media, pp. 361-362. AAAI Publications, San Jose.

Bellemain, E., & Ricklefs, R. E. (2008). Are islands the end of the colonization road? *Trends in Ecology and Evolution*, 23, 461–468.

Bittkau, C., & Comes, H. P. (2009). Molecular inference of a Late Pleistocene diversificationshift in *Nigella* s. lat. (Ranunculaceae) resulting from increased speciation in the Aegean archipelago. *Journal of Biogeography*, 36, 1346–1360.

Bloomfield, N. J., Knerr, N., & Encinas-Viso, F. (2018). A comparison of network and clustering methods to detect biogeographical regions. *Ecography*, 41, 1-10.

Borregaard, M. K., Amorim, I. R., Borges, P. A. V., Cabral, J. S., Fernández-Palacios, J. M., Field, R., Heaney, L. R., Kreft, H., Matthews, T. J., Olesen, J. M., Price, J., Rigal, F., Steinbauer, M.J., Triantis, K.A., Valente, L., Weigelt, P., & Whittaker, R.J. (2017). Oceanic island biogeography through the lens of the General Dynamic Model: assessment and prospect. *Biological Reviews*, 92, 830–852.

Carstensen D. W., Dalsgaard, B., Svenning, J. C., Rahbek, C., Fjeldså, X, Sutherland, W. J., & Olesen, J. M. (2012). Biogeographical modules and island roles: a comparison of Wallacea and the West Indies. *Journal of Biogeography*, 39, 739–749.

Carstensen, D. W., & Olesen, J. M. (2009). Wallacea and its nectarivorous birds: nestedness and modules. *Journal of Biogeography*, 36, 1540–1550.

Comes, H. P., Tribsch, A., & Bittkau, C. (2008). Plant speciation in continental islandfloras as exemplified by *Nigella* in the Aegean Archipelago. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3083–3096.

Csárdi, G., & Nepusz, T. (2006). *The igraph software package for complex network research*. InterJournal Complex Systems 1695.

Dermitzakis, D. M. (1990). Paleogeography, geodynamic processesand event stratigraphy during the late Cenozoic ofthe Aegean area. *Academia Nazionale Lincei*, 85, 263–288.

Dos Santos, D. A., Fernandez, H.R., Cuezzo, M. G., & Dominguez, E. (2008). Sympatry inference and network analysis in biogeography. *Systematic Biology*, 57, 432-448.

Doulcier, G., & Stouffer, D. (2015). *Rnetcarto: Fast Network Modularity and Roles Computation by Simulated Annealing*. R package version 0.2.4.

Edler, D., Guedes, T., Zizka, A., Rosvall, M., & Antonelli, A (2017). Infomap bioregions: interactive mapping of biogeographical regions from species distributions. *Systematic Biology*, 66, 197–204.

Fattorini, S. (2002). Biogeography of the tenebrionid beetles (Coleoptera, Tenebrionidae) on the Aegean Islands (Greece). *Journal of Biogeography*, 29, 49–67.

Fernández-Palacios, J. M. (2011). Why islands? In V. Pérez Mellado and C. Ramón (Eds.), *Islands and evolution* (vol. 19, pp. 85–109). Mahon: Institut Menorquí d'Estudis.

Ficetola, G. F., Mazel, F., & Thuiller, W. (2017). Global determinants of zoogeographical boundaries. *Nature Ecology & Evolution*, 1, 0089.

Greuter W. (1975). Historical phytogeography of the southern half of the Aegean area. In D. Jordanov, I. Bondev, W. Greuter, S. Kozuharov, B. Kuzmanov, E. Palamarev and V. Velcev (Eds.), *Problems of Balkan flora and vegetation* (pp. 17–21). Proceedings of the first international symposium on Balkan flora and vegetation, Varna, June 7–14, 1973.

Guimerá, R., & Amaral, L. A. N. (2005a). Functional cartography of complex metabolic networks. *Nature*, 433, 895–900.

Guimerá, R., & Amaral, L. A. N. (2005b). Cartography of complex networks: modules and universal roles. *Journal of Statistical Mechanics: Theory and Experiment*, P02001.

Hausdorf, B., & Hennig, C. (2005). The influence of recent geography,palaeogeography andclimate on the composition of the fauna of the centralAegean Islands. *Biological Journal of the Linnean Society*, 84, 785–795.

He, J., Kreft, H., Gao, E., Wang, Z., & Jiang, H. (2017). Patterns and drivers of zoogeographical regions of terrestrial vertebrates in China. *Journal of Biogeography,* 44, 1172–1184.

Helmus, M. R., Mahler, D. L., & Losos, J. B. (2014). Island biogeography of the Anthropocene. *Nature*, 513, 543–546.

Holt, B. G., Lessard, J. P., Borregaard, M. K., Fritz, S. A., Araujo, M. B. Dimitrov, D. S, Fabre, P-H. F., Graham, C. H., Graves, G. R., Jønsson, K. A., David Nogues-Bravo, B., Wang, Z., Whittaker, R. J., Fjeldså, J., & Rahbek, C. (2013). An update of Wallace's zoogeographic regions of the world. *Science*, 339, 74–78.

Jacomy, M. (2009). *Force-Atlas Graph Layout Algorithm*. Available at: http://gephi.org/2011/forceatlas2-the-new-version-of-our-home-brew-layout/

Jaros, U., Tribsch, A., & Comes, H. P. (2017). Diversification in continental island archipelagos: new evidence on the roles of fragmentation, colonization and gene flow on the genetic divergence of Aegean *Nigella* (Ranunculaceae). *Annals of Botany*, 121, 241–254.

Kapsimalis, V., Pavlopoulos, K., Panagiotopoulos, I., Drakopoulou, P., Vandarakis, D., Sakelariou, D., & Anagnostou, C. (2009). Geoarchaeological challenges in the Cycladescontinental shelf (Aegean Sea). *Zeitschrift für Geomorphologie*, SI 53, 169–190.

Kougioumoutzis, K., Simaiakis, S. M., & Tiniakou, A. (2014). Network biogeographical analysis of the central Aegean archipelago. *Journal of Biogeography*, 41, 1848–1858.

Kougioumoutzis, K., Valli, A.-T, Georgopoulou, E., Simaiakis, S. M., Triantis, K. A., & Trigas, P. (2017). Network biogeography of a complex island system: the Aegean archipelago revisited. *Journal of Biogeography*, 44, 651–660.

Kreft, H. & Jetz, W. (2010). A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, 37, 2029–2053.

Leprieur, F., & Oikonomou, A. (2014). The need for richness-independent measures of turnover when delineating biogeographical regions. *Journal of Biogeography*, 41, 417–420.

Lymberakis, P., & Poulakakis, N. (2010). Three continents claiming an archipelago: the evolution of Aegean's herpetofaunal diversity. *Diversity*, 2, 233–255.

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press, NJ.

Mylonas, M. (1982). *The zoogeography and ecology of the terrestrial mollusks of Cyclades*. PhD thesis, University of Athens, Greece. (in Greek, English abstract)

Mylonas, M. (1984). The influence of man: A special problem in the study of the zoogeography of terrestrial mollusks on the Aegean islands. In A. Solem and A.C. Van Bruggen (Eds.), *World-wide snails. Biogeographical studies on non-marine Mollusca* (pp. 249–259). E. J. Brill, Leiden.

Oikonomou, A., Leprieur F., & Leonardos, I. D. (2014) Biogeography of freshwater fishes of the Balkan Peninsula. *Hydrobiologia*, 738, 205–220.

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences USA*, 104, 19891–19896.

Papadopoulou, A., Anastasiou, I., Spagopoulou, F., Stalimerou, M., Terzopoulou, S., Legakis, A., Vogler, A.P. (2011). Testing the species-genetic diversity correlation in the Aegean archipelago: toward a haplotype-based macroecology? *American Naturalist*, 178, 241–255.

Poulakakis, N., Kapli, P., Lymberakis, P., Trichas, A., Vardinoyiannis, K., Sfenthourakis, S., & Mylonas, M. (2015). A review of phylogeographic analyses of animal taxa from the Aegean and surrounding regions. *Journal of Zoological Systematics and Evolutionary Research*, 53, 18–32.

Rechinger, K. H. (1943). Flora Aegaea. Flora der Inseln und Halbinseln des ägäischen Meeres. *Denkschriften, Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse*, 105, 1-184.

Rechinger, K. H. & Rechinger-Moser, F. (1951). Phytogeographia Aegaea. *Denkschriften, Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse,* 105, 1-208.

Runemark, H. (1970). The plant geography of the central Aegean. *Feddes Repertorium*, 81, 229–231.

Runemark, H. (1971). The phytogeography of the Central Aegean. *Opera Botanica*, 30, 20-28.

Sakellariou, D., & Galanidou, N. (2016). Pleistocene submerged-landscapes and Palaeolithic archaeology in the tectonicallyactive Aegean region. In J. Harff, G. Bailey and F. Luth (Eds.), *Geology and archaeology: submerged landscapes of the continental shelf* (vol. 411, pp. 145 –178). Geological Society, Special Publications, London.

Sakellariou, D., Lykousis, V., Geraga, M., Rousakis, G., & Soukisian, T. (2017). Late Pleistocene Environmental Factors of the Aegean Region (Aegean Sea Including the Hellenic Arc) and the Identification of Potential Areas for Seabed Prehistoric Sites and Landscapes. In N.C. Flemming, J. Harff, D. Moura, A. Burgess and G N. Bailey (Eds.), *Submerged Landscapes of the European Continental Shelf: Quaternary Paleoenvironments*(pp. 405-429). Wiley-Blackwell.

Sclater, P. L. (1858). On the general geographical distribution of the members of the class Aves. *Journal of the Proceedings of the Linnean Society: Zoology*, 2, 130–136.

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 and Biogeography Letters*, 5(3), 149-157.

Sfenthourakis, S., & Triantis, K. A. (2017). The Aegean archipelago: a natural laboratory of evolution, ecology and civilizations. *Journal of Biological Research-Thessaloniki*, 24, 4.

Sfenthourakis, S., Giokas, S., & Mylonas, M. (1999). Testing for nestedness in the terrestrial isopods and snails of Kyklades islands (Aegean archipelago, Greece). *Ecography*, 22, 384–395.

Simaiakis, S. M., Dretakis, M., Barboutis, C., Katritis, T., Portolou, D., & Xirouchakis, S. (2012). Breeding land birds across the Greek islands: a biogeographic study with emphasis on faunal similarity, species–area relationships and nestedness. *Journal of Ornithology*, 153, 849–60.

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., Rijsdijk, K. F., Koene, E. F. M., Norder, S. J., Van Boxel, J. H., Stocchi, P., Hammoud, C., Kougioumoutzis, K., Georgopoulou, E., Van Loon, E., Tjørve, K. M. C., & Tjørve, E. (2017). Geographic changes in the Aegean Sea since the Last Glacial Maximum: Postulating biogeographic effects of sea-level rise on islands. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 471, 108–119.

Strid, A. (1996). Phytogeographia Aegaea and the flora Hellenica database. *Annalen des Naturhistorischen Museums in Wien. Serie B für Botanik und Zoologie*, 279-289.

Strid, A. (2016). *Atlas of the Aegean flora*. Botanic Garden and Botanical Museum Berlin-Freie Universität Berlin.

Triantis, K. A., Economo, E. P., Guilhaumon, F., & Ricklefs, R. E. (2015). Diversity regulation at macro-scales: species richness on oceanic archipelagos. *Global Ecology and Biogeography*, 24, 594–605.

Triantis, K. A., & Mylonas, M. (2009). Greek Islands, Biology. In R. Gillespie and D. A. Glague (Eds.), *Encyclopedia of Islands* (pp. 388–392). University of California Press.

Triantis, K. A., & Sfenthourakis, S. (2012). Island biogeography is not a single-variable discipline: the small island effect debate. *Diversity and Distributions*, 18, 92–96.

Triantis, K. A., Senthourakis, S., & Mylonas, M. (2008). Biodiversity patterns of terrestrial isopods from two island groups in the Aegean Sea (Greece): Species–area relationship, small is land effect, and nestedness. *Ecoscience*, 15(2), 169-181.

Triantis, K. A., Vardinoyannis, K., & Mylonas, M. (2008). Biogeography, land snails and incomplete data sets: The case of three island groups in the Aegean Sea. *Journal of Natural History*, 42, 467–490.

Triantis, K. A., Whittaker, R. J., Fernández-Palacios, J. M.,& Geist, D.J. (2016). Oceanic archipelagos: a perspective on the geodynamics and biogeography of the World's smallest biotic provinces. *Frontiers of Biogeography*, 8.2, e29605.

Vilhena, D. A., & Antonelli, A. (2015). A network approach for identifying and delimiting biogeographical regions. *Nature Communications*, 6, 6848.

Trigas, P., Panitsa, M., & Tsiftsis, S. (2013). Elevational gradient of vascular plant species richness and endemism in Crete–the effect of post-isolation mountain uplift on a continental island system. *PLoS One*, 8, e59425.

von Humboldt, A., & Bonpland, A. (1807). *Essai sur la géographie des plantes : accompagné d'un tableau physique des régions équinoxiales, fondé sur des mesures exécutées, depuis le dixième degré de latitude boréale jusqu'au dixième degré de latitude australe, pendant les années 1799, 1800, 1801, 1802 et 1803*. A Paris, Chez Levrault, Schoell et compagnie, libraires, XIII.

Wallace, A. R. (1876). *The geographical distribution of animals*. Cambridge University Press, Cambridge.

Warren, B. H., Simberloff, D., Ricklefs, R. E., Aguilée, R., Condamine, F. L., Gravel, D., Morlon, H., Mouquet, N., Rosindell, J., Casquet, J., Conti, E., Cornuault, J., Fernández-Palacios, J. M., Hengl, T., Norder, S. J., Rijsdijk, K. F., Sanmartín, I., Strasberg, D., Triantis, K. A, Valente, L. M., Whittaker, R. J., Gillespie, R. G., Emerson, B. C., & Thébaud, C. (2015). Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. *Ecology Letters*, 18, 200–217.

Weigelt, P., Jetz, W., & Kreft, H. (2013). Bioclimatic and physical characterization of the World's islands. *Proceedings of the National Academy of Sciences,USA*, 110, 15307–15312.

Wettstein, O. (1953). Herpetologia Aegaea. *Sitzungsberichte der Mathematischen-Naturwissenschafftlichen Klasse Abteilung B*, 162, 651-833.

Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford: Oxford University Press.

Whittaker, R., Fernández-Palacios, J. M., Matthews, T. J., Borregaard, M. K., & Triantis, K. A. (2017). Island biogeography: Taking the long view of nature's laboratories. *Science*, 357, eaam8326.

Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, 35, 977–994.