



# Network biogeography of a complex island system: the Aegean Archipelago revisited

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## ABSTRACT

**Aim** The Aegean Archipelago has been the focal research area for identifying and testing several ecological and evolutionary patterns, yet its biogeographical subdivision has been somewhat overlooked, with the processes driving the assembly of the Aegean island plant communities still remaining largely unclear. To bridge this gap, we identify the biogeographical modules (highly linked subgroups of islands and plant taxa) within the Aegean Archipelago.

**Location** The Aegean Archipelago, Greece.

**Methods** We used a network approach to detect island biogeographical roles and modules, based on a large and detailed database including 1498 Aegean endemic and subendemic plant taxa distributed on 59 Aegean Islands and five adjacent mainland areas.

**Results** The Aegean was divided into six biogeographical modules; the network was significantly modular. None of the modules displayed all four possible biogeographical roles (connectors, module hubs, network hubs, peripherals). Six new biogeographical regions in the Aegean were identified.

**Main conclusions** The borders of the six biogeographical regions in the Aegean correspond well to the region's palaeogeographical evolution from the middle Miocene to the end of the Pleistocene. The Central Aegean acts as an ecogeographical filter for the distribution of several plant lineages across the Aegean Sea, while there seems to be a N–S-oriented biogeographical barrier in the Aegean corresponding to the palaeogeographical situation during the middle Ionian. These biogeographical barriers have been fundamental for both plants and animals.

## Keywords

Aegean, climate, connectance, dispersal, ecological network, endemism, island biogeography, modularity, palaeogeography

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## INTRODUCTION

The Aegean Archipelago is one of the largest archipelagos in the world with more than 7000 islands and islets (Triantis & Mylonas, 2009). Its high environmental and topographical heterogeneity, complex geological and palaeogeographical history, as well as high diversity and endemism, render it an ideal stage for biodiversity and biogeographical studies (Strid, 1996). The Aegean has long fascinated biogeographers, as it lies at the crossroads of three different biogeographical regions, namely Europe, Asia and Africa (Triantis & Mylonas, 2009).

The modern botanical exploration of the Aegean Islands dates back to the late 18th century (see Lack & Maberley, 1999). The substantial plant distribution data collected by pioneer botanists working in the Aegean enabled Turrill (1929) to first divide the area in six phytogeographical regions. Later on, Rechinger (1943, 1950) first addressed the phytogeographical peculiarities of the Aegean (e.g. Kykladenfenster, i.e. the absence of several taxa from the Central Aegean that are present in the Greek mainland and in the East Aegean Islands). Both noticed the abrupt phytogeographical differences between the Kiklades and the East Aegean Islands, drew the phytogeographical line dividing

Asia from Europe (i.e. Rechinger's line) and laid the foundations of the Aegean's prevailing phytogeographical subdivision (Rechinger & Rechinger-Moser, 1951). Later, Runemark (1970) and Greuter (1971) focused on the Central and South Aegean, respectively, and first examined the effect of the Aegean's complex palaeogeographical history on the plants' distributional patterns. Nearly three decades later, Strid (1996) based on Rechinger (1943) and the total number of native taxa then known to occur in Greece, divided Greece in 13 phytogeographical regions. In the Aegean, he identified five phytogeographical regions: Kiklades, Kriti-Karpathos, East, North and West Aegean Islands (Kik, KK, EAe, NAe and WAe respectively).

Even though intensive fieldwork has taken place in the Aegean phytogeographical regions of Greece (Dimopoulos *et al.*, 2013) and phytogeographical studies for the East (Panitsa *et al.*, 2010), South (Kagiampaki *et al.*, 2011) and Central Aegean Islands (Kougiumoutzis & Tiniakou, 2014) have been carried out focusing on both the total and endemic species richness, our understanding of the processes driving the assembly of the Aegean island communities is still far from complete. It was not until very recently that the phytogeographical subdivision within the Central Aegean Islands came into the spotlight (Kougiumoutzis *et al.*, 2014), while the phytogeographical subdivision of areas as heterogeneous as EAe and the South Aegean Island Arc (the island chain connecting Peloponnese with Anatolia) have never been treated before.

The identification of biogeographical regions (geographically distinct assemblages of species and communities) is a critical step for unveiling the processes establishing species diversity (Vilhena & Antonelli, 2015). Identification of biogeographical regions has mainly been based on empirical knowledge, but recently this was replaced by methodologies based on beta diversity (Kreft & Jetz, 2010), as well as by more analytical approaches based on networks (Carstensen & Olesen, 2009). Such delimitation within archipelagos involves species distributions across an island system that can be treated as an island-species network. Islands may differ regarding their role in connecting the biotas across an archipelago; differences in the geophysical characteristics, geological origin, spatial arrangement within the archipelago and palaeogeographical evolution of each respective island establish its biogeographical role. In this context, network analysis is a promising and powerful tool for understanding island connectivity (Dos Santos *et al.*, 2008), as it provides a holistic approach, free of a priori dataset assumptions, which is better than pairwise analyses for assessing interactions within complex datasets (Proulx *et al.*, 2005). Network biogeographical analysis based on species distributions is an objective, optimal and emerging method for the identification of biogeographical regions within an archipelago (Carstensen *et al.*, 2012, 2013; Dalsgaard *et al.*, 2014; Kougiumoutzis *et al.*, 2014). NETCARTO (Guimerá & Amaral, 2005) is a module-detecting algorithm, used among others, in ecological (Olesen *et al.*, 2007) and biogeographical studies (Carstensen

*et al.*, 2012, 2013). Apart from identifying biogeographical modules, NETCARTO also classifies islands according to their linkage patterns, their topological position and biogeographical role in the island-plant taxa network. This provides information on how the individual islands contribute to biogeographical connectivity, both within each biogeographical module and across the entire archipelago (Carstensen *et al.*, 2012). Finally, NETCARTO detects fine-grained biogeographical patterns (Carstensen & Olesen, 2009) and identifies the spatial importance of islands beyond that based on species richness patterns.

To our knowledge, this is the first study focusing on the compartmentalization and phytogeography of the Aegean Archipelago, based on a novel methodology and taking into account the effect of continental areas in shaping island biogeographical patterns. Thus, the aim of this study is to identify biogeographical groups of islands and closely linked plant taxa, as well as their roles in one of the most diverse archipelagos of the globe.

## MATERIALS AND METHODS

### Palaeogeographical history of the Aegean

Most Aegean islands are of continental origin, except those belonging to the South Aegean Volcanic Arc (SAVA): Anafi, Kimolos, Milos, Nisyros, Polyaeos and Santorini (for a thorough review on the SAVA, see Francalanci *et al.*, 2005).

The palaeogeographical history of the Aegean is relatively recent and rather complex, determined by three main geological events that created important dispersal barriers: (1) the formation of the mid-Aegean trench (MAT), (2) the isolation of Kriti from Peloponnese after the Messinian salinity crisis (MSC) and (3) the separation of Karpathos' island group from Rhodos in the Pliocene. The fragmentation of Ägäis (the present-day Aegean, a then continuous large land-mass) started during the Middle and Upper Miocene (Creutzburg, 1966; Dermitzakis, 1990). The opening of the MAT was initiated by the sea intrusion that separated Kriti from Karpathos' island complex 12 Ma. This initial split then bifurcated, forming the MAT at a N-S axis, reaching up to Thasos (9 Ma) and separated Kiklades from the East Aegean Islands, while a second split (10-9 Ma) separated Kiklades from Kriti and the Peloponnese (Dermitzakis, 1990). During the MSC (5.97-5.33 Ma, Manzi *et al.*, 2013), the entire Mediterranean Basin dried up (Krijgsman *et al.*, 1999) and the Aegean Islands became mountains surrounded by steppes or saline deserts, thus enabling land-dispersal. Nevertheless, Kriti was isolated from the rest of the Aegean by extensive saline deserts or saline/hypersaline lakes, while a similar barrier remained throughout the MSC at the area of the MAT (Schüle, 1993). After the MSC, Kriti was permanently isolated from the rest of the Aegean (Meulenkamp *et al.*, 1988). The Karpathos' island complex was joined with Rhodos and Anatolia in Lower Pliocene (Daams & van der Weerd, 1980), but remained isolated since the Upper

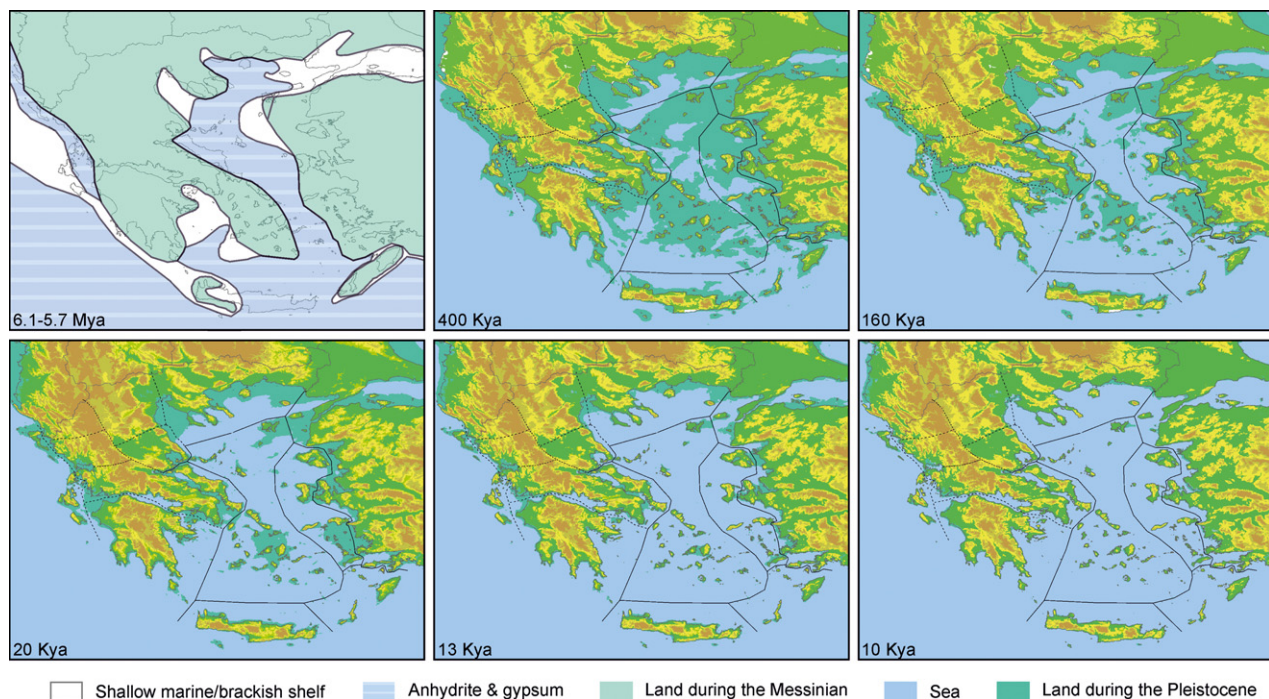
Pliocene (Dermitzakis, 1990). Rhodes was permanently separated from Anatolia at the Plio/Pleistocene boundary (Kuss, 1975). During the Pleistocene glacial and interglacial periods, connections among many Aegean islands and adjacent mainland were established or broken in a labyrinthine sequence of events (Fig. 1). At 480–250 ka, the North Aegean Trough (NAT) was isolated from the open sea and the North Aegean Island Bridge connected mainland Greece with NW Anatolia. A large lake, with several deep basins, occupied the Central Aegean and the Central Aegean Island Bridge connected mainland Greece with Anatolia. At 180–140 ka, mainland Greece was isolated from Anatolia and the East Aegean Islands formed three distinct Anatolian peninsulas in a N–S axis. At 30–18 ka, some of the Aegean Islands started to acquire their present configuration and at *c.* 8 ka, all of the Aegean Islands were finally formed (for a thorough review see Kapsimalis *et al.*, 2009; Sakellariou & Galanidou, 2016).

## Data

We compiled a presence/absence island/mainland-plant matrix for the Aegean Archipelago, containing 64 islands/mainland areas [59 Aegean islands and 5 Greek adjacent mainland areas: the phytogeographical areas of Peloponnese, Sterea Ellas, north-east, north-central and east-central Greece (Pe, StE, NE, NC and EC, thereafter) *sensu* Strid & Tan (1997)] and 1498 Aegean endemic and subendemic plant taxa. The Aegean endemics and subendemics constitute a significant floristic component of all Aegean islands and their

distribution patterns emit a strong phytogeographical signal (Rechinger, 1950; Greuter, 1975).

We created an extensive and detailed bibliographical database for the Aegean Archipelago (see Appendix S1 in Supporting Information) to compile our matrix. The total number of taxa of a single island is the sum of (1) the taxa that have a distribution range restricted to the Aegean Islands (i.e. Aegean endemics – ΑΕ) and (2) the taxa that have a distribution range restricted to the Aegean Archipelago and one of the adjacent (Greek or Anatolian) continental areas (i.e. Aegean subendemics). The single island endemics (SIE) and the taxa that are endemic to a single phytogeographical region are subsets of the Aegean endemics. The chorological status of the taxa is based on Dimopoulos *et al.* (2013) and Strid (2016). The quality of the available plant distributional data from mainland Greece does not allow the extraction of reliable conclusions regarding the subdivision of continental Greece, which is beyond the scope of the present paper. Thus, we accepted the boundaries of the mainland phytogeographical regions of Greece as circumscribed by Strid & Tan (1997) and we included them in our analyses only to investigate the effect of continental areas in shaping the Aegean biogeographical modules. We did not include in the analysis the total number of the native plant taxa present in our dataset because when dealing with phytogeographical issues in the Aegean only the range restricted taxa, rather than the whole flora, is phytogeographically meaningful and informative (Greuter, 1975).



**Figure 1** The Aegean region from the Neogene to present, as well as the identified biogeographical modules. Drawing based on the current geography. The simplified depiction of the Aegean region during the Messinian is based on Popov *et al.* (2004) (for colouration see the online version of this article). From top-left to bottom right: a–f.



## Simulated annealing

We constructed the island/mainland-plant taxa network from the presence/absence matrix. We followed the same methodology as Kougioumoutzis *et al.* (2014) did (see Appendix S1 for a thorough explanation of this method). We followed Carstensen *et al.*'s (2012) nomenclature regarding *l* (local topological linkage) and *r* (regional topological linkage) and the role classification proposed by Guimerá & Amaral (2005), modified by Olesen *et al.* (2007). Thus, we sorted all plant taxa and islands into four kinds of roles, namely peripherals, connectors, module hubs and network hubs (for a thorough explanation of the biogeographical roles, see Appendix S1). The latter three are termed generalists in the network.

## Best subset regression analysis

We applied a best subset regression analysis (Burnham & Anderson, 2002) to explore the effect of key biological, geographical and climatic variables on an island's local (*l*) and regional (*r*) topological linkage. We used Akaike's information criterion (AIC) to identify the minimum adequate models. This process also allowed calculating the relative importance for each explanatory variable, which captured the percentage of variation explained by each factor when the other factors were held constant. The variance inflator factors (VIF) were below 2.5, thus indicating that multicollinearity was not a problem in any of our obtained models. We used Moran's *I* coefficient to investigate the spatial autocorrelation of the regression residuals (Diniz-Filho *et al.*, 2003). Moran's *I* coefficient statistics were calculated in SAM 4.0 (Rangel *et al.*, 2010). No spatial autocorrelation was detected in any of the models.

The explanatory variables were island area (*A* - km<sup>2</sup>), maximum elevation (*E* - m), distance to nearest mainland and island (*D<sub>m</sub>* and *D<sub>i</sub>* respectively - km), number of geological substrates (*G*), as well as present and Quaternary mean annual temperature and precipitation (*T<sub>p</sub>*, *T<sub>Q</sub>*, *P<sub>p</sub>*, *P<sub>Q</sub>*,

respectively). *A* and *E* were determined from 1:50,000 scale digital topographical maps obtained from the Hellenic Military Geographical Service. *G* was compiled from the 1:500,000 scale Geological Map of Greece (Bornovas & Rongogianni-Tsiambaou, 1983), while Google Earth was used to compute *D<sub>i</sub>* and *D<sub>m</sub>*. We used WorldClim 30-arc second climate products (Hijmans *et al.*, 2005) to calculate the climatic variables; *T<sub>Q</sub>* and *P<sub>Q</sub>* were obtained from the CCSM4 model and were statistically downscaled to a 2.5-arc minute resolution (Hijmans *et al.*, 2005).

We log<sub>10</sub>-transformed all the variables to normalize their distribution and improve the linearity of the relationships in the regression models. All correlation and regression analyses were carried out in the R 3.2.2 computing environment (R Core Team 2015) using core functions and functions from the 'leaps' (Lumley, 2009) package.

## RESULTS

### Simulated annealing

The network was significantly modular ( $M_{\text{Aegean}} = 0.549$ ,  $M_{\text{Aegean-r}} = 0.535$ ,  $P = 0.0012$ ). Most links in the Aegean are among islands/areas within the same module (61.68%). Mean module and network connectance (as proposed by Olesen *et al.*, 2007), as well as mean betweenness centrality and intermodule distance are presented in Table 1.

Six distinct biogeographical modules were detected (Figs 1 & S1) and module names are written in small caps as follows. SOUTH MAINLAND & ISLANDS (SMI) consists of Kythira, Antikythira, Elafonissos, Pe, StE and Evvia, while the Kiklades together with the Northern Sporades and Limnos comprise CENTRAL AEGEAN (CAE). Rhodos and Karpathos island complexes, together with Nisyros and Tilos, comprise SOUTH-EASTERN AEGEAN (SE-AE), while Lesvos, Chios, Samos, Kos, Ikaria, Kalymnos, Leros and Patmos comprise NORTH-EASTERN AEGEAN (NE-AE). NORTH MAINLAND & ISLANDS (NMI) consists of Thasos, Samothraki, EC, NC and NE. Finally, Kriti, the largest island in the

**Table 1** Description of each biogeographical module in the Aegean Archipelago and their network properties. Module endemics is the percentage of endemic vascular plant taxa designated to a given module that are not distributed on islands outside this module. SIE and AE are the number of the single island endemics and Aegean endemics (endemic taxa occurring in more than one phytogeographical regions of the Aegean), respectively. The percentage of each module's SIE and AE is shown within the parenthesis (the denominator corresponds to the total number of native taxa present on the islands comprising each module).  $CM_m$ ,  $CN_m$ ,  $ID_m$ ,  $iBCI_m$  and  $tBCI_m$  are the mean module connectance, network connectance, intermodule distance, island and taxa betweenness centrality respectively.

Module	No. of islands	No. of taxa	Mean number of taxa per site	Module endemics (%)	SIE	AE	$CM_m$	$CN_m$	$iBCI_m$	$tBCI_m$	$ID_m$
SMI	6	586	97.67	84.60	44 (2.22)	87 (4.40)	–	–	39049.9	37.5	–
NMI	5	285	57.00	79.60	17 (0.98)	19 (1.10)	–	–	23861.7	326.5	–
KR	2	229	114.50	87.80	170 (9.16)	201 (10.84)	–	–	64838.0	168.0	–
SE-AE	8	122	15.25	51.60	15 (0.93)	71 (4.42)	–	–	7797.6	391.4	–
NE-AE	8	148	18.50	68.90	23 (1.13)	42 (2.07)	–	–	14257.5	390.7	–
CAE	35	128	3.66	43.00	18 (0.99)	88 (4.83)	–	–	3483.7	1043.4	–
Total	64	1498	23.41	–	287 (8.09)	508 (14.32)	0.034	5.53	12213.4	262.1	27.37

archipelago, comprises together with Gavdos KRIT (KR). KR has the largest species-island ratio and percentage of module endemics, while CAE has the smallest values for these metrics (Table 1). NE-AE and CAE were the most closely connected modules, while NMI was the most isolated (see Table S2, Appendix S2 in Supporting Information). Pe and StE have the highest  $l$  and BCI values, respectively (Kriti has the highest values for those two metrics among the Aegean Islands), while Skiathos and Antiparos have the lowest  $l$  and BCI values respectively (see Table S3 in Appendix S2).

On average, a module contains  $10.67 \pm 11.07$  islands/areas and  $249.67 \pm 161.37$  taxa with a species-island ratio of 51.10, module endemism of  $69.30 \pm 16.78\%$  and module BCI value of  $901.583 \pm 357.03$ . Thirty-eight islands/areas are classified as peripherals, 21 as module hubs and five as connectors (Fig. 2). The vast majority of the plant taxa (96.67%) are peripherals – 79.01% of these did not have links outside their own module (module endemics,  $r = 0$ ) – while 3.33% are connectors (see Appendix S3 in Supporting Information). All the modules – except KR – have very low percentages of SIE and AE (Table 1); KR and SE-AE have the highest and lowest percentage of SIE respectively (Table 1).

### Best subset regression

$A$ ,  $E$  and  $D_m$  were retained in the optimal model for  $l$ , while  $E$  together with  $P_p$ ,  $T_p$ ,  $D_i$  and  $D_m$  were retained in the optimal model for  $r$  (Table S4).  $A$  and  $E$  were the most important determinants of  $l$  and  $r$ , respectively. More specifically, high- $l$  islands were large, high-elevation islands situated away from the mainland, while high- $r$  islands were high-elevation islands situated near the mainland with wetter and warmer climate. An island's  $l$  was strongly correlated with endemic richness (Table S5);  $r$  was strongly correlated with SIE richness (Figs S2–S9).

## DISCUSSION

### Biogeographical modules in the Aegean

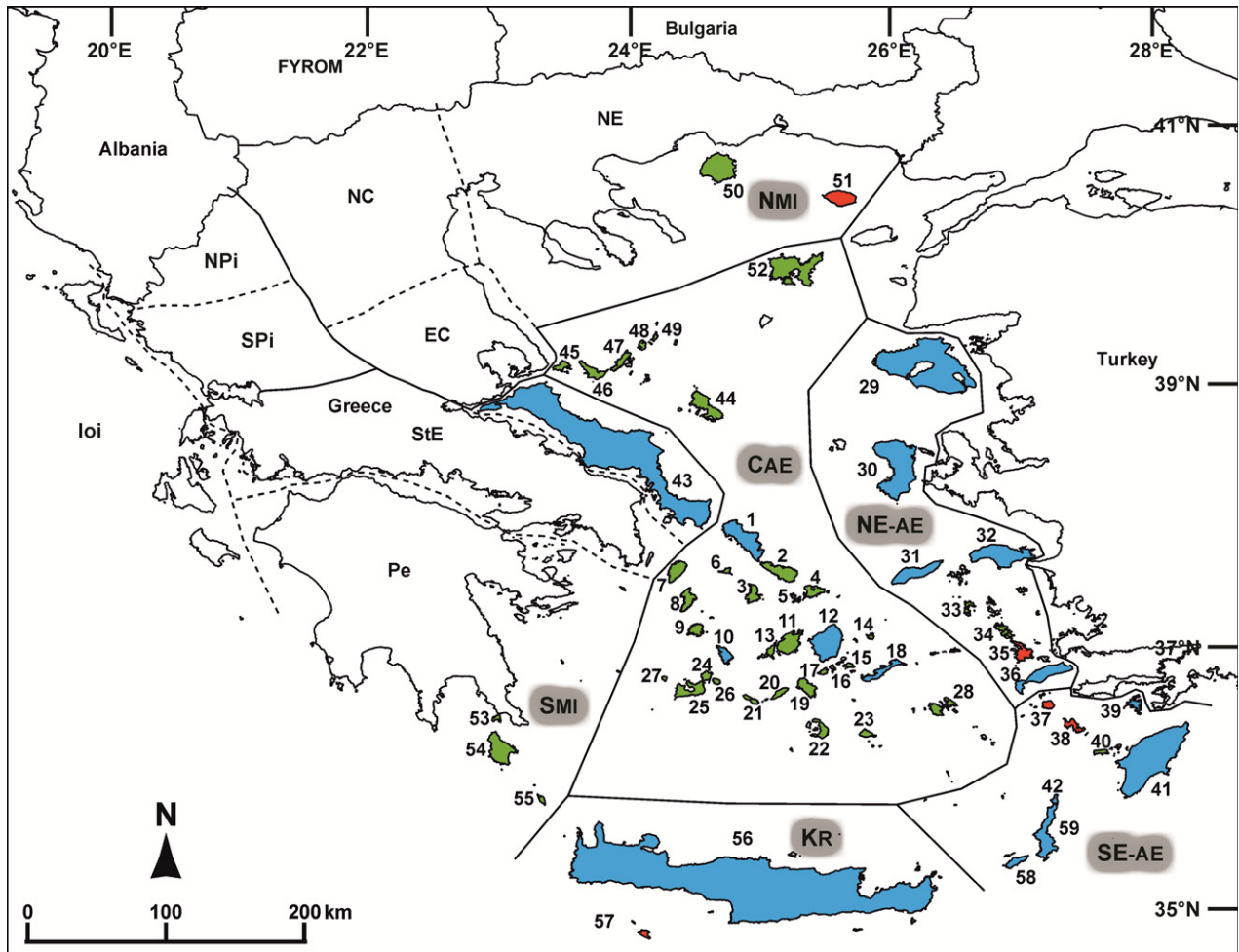
We assessed for the first time the biogeographical regions of the whole Aegean Archipelago and we identified the role of mainland areas in driving island biogeographical patterns via a network optimization approach. In large archipelagos, such as the Aegean, many species immigrating to an island will be species from the adjacent continental mainland areas and from nearby, usually larger islands (e.g. Whittaker & Fernández-Palacios, 2007). We identified six large biogeographical modules in the Aegean that build upon and improve previous classifications (Turrill, 1929; Rechinger & Rechinger-Moser, 1951; Strid, 1996). The existence of a continuous phytogeographical region of the West Aegean Islands (sensu Strid, 1996) is not supported by our results (Fig. 2): (1) Evvia, which is phytogeographically very well separated from the Northern Sporades, constitutes together with StE, Pe and the Kythira's island complex SM1 and (2) the Northern

Sporades together with Limnos and the Kiklades constitute CAE. Secondly, EAe is split in a N–S axis: the island chain from Lesvos to Kos constitutes NE-AE, while the rest of the East Aegean Islands form together with the Karpathos' island complex SE-AE. Furthermore, due to the previous split, Kriti is established as a distinct phytogeographical region in the Aegean (KR), separated from the Karpathos' island complex. Finally, Rechinger's line, separating Kik from EAe, and practically Asia from Europe, seems to represent a rather weaker than previously thought biogeographical barrier, according to the intermodule distance matrix (see Table S2), as CAE is more closely connected to the East Aegean islands than to any other region. The aforementioned differences can be the result of the different techniques used (i.e. network versus cluster analysis), as according to Carstensen & Olesen (2009), a network approach based on simulated annealing is more suitable for detecting fine-grained biogeographical patterns. Evidently, this appears to be also true for coarse-grained biogeographical patterns.

The complex geological history of the Aegean has played a significant role in shaping the area's biogeographical patterns, as suggested by both plants (e.g. Crowl *et al.*, 2015) and animals (e.g. Poulakakis *et al.*, 2014). The topology derived herein coincides largely with the Aegean's palaeogeographical history and its evolution during the later stages of the Neogene and the Quaternary (Fig. 1a–f – see also the figures in Lymberakis & Poulakakis, 2010 and Sakellariou & Galanidou, 2016). Two main distributional and (palaeo-)geographical barriers seem to exist in the Aegean Archipelago: the MAT and the NAT. The formation of the MAT plays a critical role in shaping the Aegean's biogeographical patterns; this ancient and predominant barrier, which has also affected animal distribution patterns (e.g. Poulakakis *et al.*, 2014), is stronger in its southern and geologically older tip, as it distinctively separates (Table S2) Kriti from Karpathos, the Central Aegean and the Peloponnese (KR formation: *c.* 11.6–5.3 Ma). The MAT does deserve some merit regarding the phytogeographical separation of the Central Aegean from the East Aegean (SE-AE formation: *c.* 2.6 Ma; CAE formation: *c.* 480 ka – Fig. 1b), yet its power appears to be dwindling in a S–N axis (Table S2). In the North Aegean, the plant distribution patterns have been shaped by the interplay between the MAT and the NAT, with the latter gradually replacing the former as it heads towards the northern Greek mainland. The NAT constitutes an insurmountable barrier (Table S2, Fig. S1): the North Aegean Islands have very low affinities with the Aegean Islands situated south of the NAT and despite their close geographical proximity, Thasos and Samothraki belong to a different phytogeographical region than Limnos. This could be attributed to the isolation of Thasos and Samothraki from northern Greece during the latter phases of the Last Glacial Maximum (LGM, *c.* 13 ka – Fig. 1f). Moreover, NE-AE was practically formed at *c.* 10 ka, when all the islands comprising it were at last separated from Asia Minor (Fig. 1f). Furthermore, the long-lasting separation of Evvia from the Northern Sporades (Sakellariou &

Galanidou, 2016), along with its large size, mountainous landscape and environmental complexity, explain why Evvia is biogeographically separated from this island complex. This concurs with previous studies showing that Quaternary sea-level oscillations, as well as plate tectonic dynamics have influenced the current biogeographical structure of the Aegean (e.g. Cellinese *et al.*, 2009; Kougiumoutzis *et al.*, 2014). Moreover, our results lend weight to the hypothesis that nearby islands subject to fusion/fission cycles will share more species than comparable island groups that were never physically linked (Fernández-Palacios *et al.*, 2016). In particular, it could be argued that the spatial configuration of the Aegean Archipelago during the LGM and/or earlier glacials, (e.g. the Riss glaciation) has had a strong and detectable

impact on the plant species' distribution and evolutionary patterns (e.g. as in the *Nigella arvensis* complex – Bittkau & Comes, 2009 and the *Brassica cretica* complex – Edh *et al.*, 2007). CAE is highly intercorrelated with nearly all the Aegean Islands, except for Kriti, Thasos and Samothraki (see Table S2), a phenomenon probably reflecting the recent connections and close proximity of these island masses during the Quaternary glaciations, in contrast to the weak biogeographical relationships they display with islands that separated early in the formation of the Aegean Archipelago. CAE thus plays a central biogeographical role in the Aegean Archipelago, as its exceptionally high mean intermodule distance suggests, and actually seems to constitute a transitional biogeographical zone between Asia and Europe, filtering the



**Figure 2** The Aegean Islands, their role-space and the phylogeographical areas included in this study. Numbers correspond to the islands as follows: 1. Andros, 2. Tinos, 3. Syros, 4. Mykonos, 5. Rinia, 6. Gyaros, 7. Kea., 8. Kythnos, 9. Serifos, 10. Sifnos, 11. Paros, 12. Naxos, 13. Antiparos, 14. Donoussa, 15. Keros, 16. Schinoussa, 17. Iraklia, 18. Amorgos, 19. Ios, 20. Sikinos, 21. Folegandros, 22. Santorini, 23. Anafi, 24. Kimolos, 25. Milos, 26. Polyagios, 27. Antimilos, 28. Astypalaea, 29. Lesvos, 30. Chios, 31. Ikaria, 32. Samos, 33. Patmos, 34. Leros, 35. Kalymnos, 36. Kos, 37. Nisyros, 38. Tilos, 39. Symi, 40. Chalki, 41. Rhodos, 42. Saria, 43. Evvia, 44. Skyros, 45. Skiathos, 46. Skopelos, 47. Alonissos, 48. Kyra Panagia, 49. Gioura, 50. Thasos, 51. Samothraki, 52. Limnos, 53. Elafonissos, 54. Kythira, 55. Antikythira, 56. Kriti, 57. Gavdos, 58. Kasos, 59. Karpathos. NMI: NORTH MAINLAND & ISLANDS, CAE: CENTRAL AEGEAN, KR: KRITI, SMI: SOUTH MAINLAND & ISLANDS, SE-AE: SOUTH-EASTERN AEGEAN, NE-AE: NORTH-EASTERN AEGEAN. Dashed lines indicate the borders of the mainland phylogeographical areas of Greece. Module hub, connector and peripheral islands are shown in blue, orange and green, respectively (for colouration see the online version of this article).

distribution of taxa originating from mainland Greece, Anatolia, Kriti and the Northern Aegean. Finally, our results seem to support the notion that high spatial connectivity increases immigration rates and homogenizes the archipelagic flora, while reducing the number of SIE (e.g. Borregaard *et al.*, 2016).

There is also a strong climatic differentiation present in the Aegean (Gouvas & Sakellarios, 2011 –  $F = 2.9$ ,  $P < 0.05$ ), affecting both the plant distribution and species richness patterns, as well as the diversification patterns in the region (Kougioumoutzis & Tiniakou, 2014; Crowl *et al.*, 2015). This climatic differentiation has also affected the diversity patterns of  $l$  and  $r$  (see Island roles and characteristics below) and climate has strongly influenced the plant species' ranges in Europe (Normand *et al.*, 2011). The modules' borders reminiscent the Aegean's past and present climatic compartmentalization (see Figs S10–13). This is in accordance with the fact that the climatic differences between Kik and its surrounding phytogeographical regions are responsible for the absence of several Peloponnesian and East Aegean endemics from the area (Kougioumoutzis & Tiniakou, 2014). Moreover, our results corroborate the hypothesis that islands receive colonizers from climatically similar areas (Weigelt & Kreft, 2013), since postglacial accessibility to places with suitable conditions is an especially important factor for small-range species in southern Europe (Normand *et al.*, 2011): the contemporary distributions of numerous Aegean endemic plants (e.g. *Asyneuma giganteum*, *Limonium sitiicum* and *Lomelosia variifolia* in Karpathos' and Rhodos' island groups to name a few) reflect the effects of the palaeogeographical evolution and climatic compartmentalization in the formation of plant assemblages in the Aegean Islands.

### Island roles and characteristics

In the Aegean, as well as in other archipelagos (Carstensen *et al.*, 2012; Dalsgaard *et al.*, 2014), the island biogeographical network roles are significantly correlated with island size, elevation and isolation. Area and elevation are the major drivers of plant diversity patterns in the Aegean (Kallimanis *et al.*, 2011) and play the most important role regarding the coherence of each individual module (Table S5), as  $l$  is interpreted as the number of species from the local flora (within-module) that an island shares with other islands from the same module (Carstensen *et al.*, 2012). The value of  $r$ , on the other hand, is a measure of how widely an island's species are shared with islands in other modules (Carstensen *et al.*, 2012); it seems that the interplay between elevation, precipitation and distance to mainland are shaping the potential species pool for each island (i.e. the among-modules shared species). Islands far from the nearest mainland had higher  $r$ -values, as a large part of the species reaching them are probably generalists and good dispersers, and therefore will be widely distributed in the Aegean. The a posteriori analysis of the  $l$  and  $r$  patterns in the new Aegean phytogeographical areas (Tables S6–S8) revealed that they are affected by differentially weighted

factors. More specifically, mean annual precipitation has contrasting effects on the East Aegean modules (Tables S7 & S8) and seems to homogenize the Aegean flora, by providing the suitable climatic conditions for the immigration and establishment of endemic and subendemic taxa originating from wetter phytogeographical areas (e.g. NE-AE, Pe, StE, NE, Asia Minor) that do not prefer the water-deficient environments of SE-AE and CAE.

Non-hub (low- $l$ ) islands have been interpreted as sink islands, which tend to be small, less heterogeneous, with low *in situ* speciation rate and endemism, while hub (high- $l$ ) islands could be regarded as speciation centres (Carstensen *et al.*, 2012). Only 27% of the Aegean Islands are considered hub islands (Table S3), reflecting the strong biogeographical connections among all the detected modules. High- $l$  islands in the Aegean correlate strongly with regional and local endemic richness (Table S5) and they are large, environmentally complex islands with many SIE, usually situated close to the mainland; they act as sources for the surrounding smaller islands and define the biogeographical modules (Carstensen *et al.*, 2012; Dalsgaard *et al.*, 2014). On the other hand, Aegean high- $r$  islands are rather smaller, lower, wetter and relatively far from the mainland and less species-rich than hub islands (see Appendix S2).

In general, most of the Aegean hub islands are continental-shelf islands hosting a large number of Greek or Anatolian taxa with a restricted distribution in a single Aegean module (module-pseudoendemics). Some of them, i.e. Evvia and Samos, have a dual role, as they not only host many regional endemics, but also numerous SIE. The rest of the hub islands can be regarded as genuine hotspots of Aegean endemism and they have acted as speciation centres and/or refugia for the *in situ* evolved Aegean endemics (i.e. Kriti, Karpathos, Naxos, Amorgos, Ikaria and Rhodos). The strong correlation of  $l$  primarily to area and elevation reflects the high significance of these variables in the differentiation of the Aegean plants (e.g. Trigas *et al.*, 2013; Steinbauer *et al.*, 2016). Only five islands were classified as connectors, which can be interpreted as stepping stones for dispersing species (Carstensen *et al.*, 2012).

KR and CAE are the most and less endemic species-rich modules of the Aegean Islands, respectively (Table 1), actually reflecting the effect of area and isolation in the plant species richness patterns in the Aegean. KR, the archipelago's oldest and most isolated module has the highest module endemism in the Aegean Islands. This is because the islands comprising this module have a long isolation history and large elevation range, reflecting high environmental heterogeneity, factors known to positively affect the Aegean endemic taxa's distribution in the region (Kagiampaki *et al.*, 2011), as well as the diversification rate in the Aegean (Trigas *et al.*, 2013).

Among the insular areas, Kriti has by far the highest BCI value, followed by Samos and Andros (Table S3). The higher the node's BCI value, the more influential the node is because it functions as a junction for communication within the network (Brandes, 2001). In this context, these three



islands are the corner-stones for the network's coherence, connecting all the modules together, acting both as speciation centres (mainly Kriti) and source islands to the other islands of the network.

## CONCLUSIONS

Network analysis seems to be a powerful tool in detecting both coarse- and fine-grained biogeographical patterns; it accurately depicts the biogeographical structure of small (i.e. Kougioumoutzis *et al.*, 2014 – network size: 3498) and very large (this study – network size: 95872) datasets. The Mediterranean Basin's complex palaeogeology and palaeoclimatology has resulted in a reticulate biogeographical history in which biotas repeatedly fragmented and merged as dispersal barriers appeared and disappeared through time (Nieto Feliner, 2014 and references therein). Moreover, present-day species distributions have been influenced by a history of changing surface area, connectivity and isolation driven by sea-level rise (Rijsdijk *et al.*, 2014). These trends are also apparent in the Aegean Sea, as its plant distribution patterns reflect the area's palaeogeographical history and evolution from the middle Miocene until the end of the Pleistocene. As a result, six new phylogeographical regions were identified in the Aegean. It seems that continental Greece has played a vital role in the biogeographical structure of the Aegean and the identified module borders indicate the main borderline for which islands are sinks or stepping stones for migration and colonization from the surrounding continents, confirming and extending the findings of previous studies (e.g. Kougioumoutzis *et al.*, 2014). Furthermore, the animal and plant distribution patterns in the Aegean seem to be affected by the same biogeographical barriers: the mid-Aegean trench and the North Aegean Trough. The Central Aegean (CAE), an ecologically saturated region, acts as an ecogeographical filter in the Aegean for the distribution of several plant lineages and as a transitional biogeographical zone between the Greek mainland and the East Aegean Islands. Our results support the recent view that the sea-level cycles during glacial and interglacials influence the biogeographical processes shaping island biotas (Fernández-Palacios *et al.*, 2016; Weigelt *et al.*, 2016). There is also a resemblance between the phylogeographical compartmentalization of the Aegean both locally and regionally with the Aegean's past and present climatic compartmentalization. Finally, the island biogeographical network roles are mainly determined by area and elevation, as well as geographical isolation, however, contrasting climate regimes seem to affect an island's network position in the Aegean.

## REFERENCES

- Bittkau, C. & Comes, H.P. (2009) Molecular inference of a Late Pleistocene diversification shift in *Nigella* s. lat. (Ranunculaceae) resulting from increased speciation in the Aegean archipelago. *Journal of Biogeography*, **36**, 1346–1360.
- Bornovas, I. & Rondogianni-Tsiambaou, T. (1983) *Geological Map of Greece. Scale 1:500,000*, 2nd edn. Institute of Geology and Mineral Exploration Division of General Geology and Economic Geology, Athens.
- 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. (2016) Oceanic island biogeography through the lens of the general dynamic model: assessment and prospect. *Biological Reviews*. doi:10.1111/brv.12256.
- Brandes, U. (2001) A faster algorithm for betweenness centrality. *Journal of Mathematical Sociology*, **25**, 163–177.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical-theoretical approach*, 2nd edn. Springer, New York.
- Carstensen, D.W. & Olesen, J.M. (2009) Wallacea and its nectarivorous birds: nestedness and modules. *Journal of Biogeography*, **36**, 1540–1550.
- Carstensen, D.W., Dalsgaard, B., Svenning, J.C., Rahbek, C., Fjeldsâ, J., 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., Dalsgaard, B., Svenning, J.C., Rahbek, C., Fjeldsâ, J., Sutherland, W.J. & Olesen, J.M. (2013) The functional biogeography of species: biogeographical species roles of birds in Wallacea and the West Indies. *Ecography*, **36**, 1097–1105.
- Cellinese, N., Smith, S.A., Edwards, E.J., Kim, S.T., Haberle, R.C., Avramakis, M. & Donoche, M.J. (2009) Historical biogeography of the endemic Campanulaceae of Crete. *Journal of Biogeography*, **36**, 1253–1269.
- Creutzburg, H. (1966) Die südägäische Inselbrücke. *Erdkunde*, **20**, 20–30.
- Crowl, A., Visger, C.J., Mansion, G., Hand, R., Wu, H.-H., Kamari, G., Phitos, D. & Cellinese, N. (2015) Evolution and biogeography of the endemic *Roucela* complex (Campanulaceae: Campanula) in the Eastern Mediterranean. *Ecology and Evolution*, **5**, 5329–5343.
- Daams, R. & van der Weerd, A.V. (1980) Early Pliocene small mammals from the Aegean island of Karpathos (Greece) and their paleogeographic significance. *Geologie en Mijnbouw*, **59**, 327–331.
- Dalsgaard, B., Carstensen, D.W., Fjeldsâ, J., Maruyama, P.K., Rahbek, C., Sandel, B., Sonne, J., Svenning, J.-C., Wang, Z. & Sutherland, W.J. (2014) Determinants of bird species richness, endemism, and island network roles in Wallacea and the West Indies: is geography sufficient or does current and historical climate matter? *Ecology and Evolution*, **20**, 4019–4031.
- Dermitzakis, D.M. (1990) Paleogeography, geodynamic processes and event stratigraphy during the late Cenozoic of the Aegean area. *Accademia Nazionale Lincei*, **85**, 263–288.
- Dimopoulos, P., Raus, Th, Bergmeier, E., Constantinidis, Th, Iatrou, G., Kokkini, S., Strid, A. & Tzanoudakis, D. (2013)



- Vascular plants of Greece. An annotated checklist.* Botanic Garden and Botanical Museum Berlin-Dahlem, Berlin, Hellenic Botanical Society, Athens.
- Diniz-Filho, J.A.F., Bini, L.M. & Hawkings, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53–64.
- Dos Santos, D.A., Fernandez, H.R., Cuezco, M.G. & Dominguez, E. (2008) Sympatry inference and network analysis in biogeography. *Systematic Biology*, **57**, 432–448.
- Edh, K., Widén, B. & Ceplitis, A. (2007) Nuclear and chloroplast microsatellites reveal extreme population differentiation and limited gene flow in the Aegean endemic *Brassica cretica* (Brassicaceae). *Molecular Ecology*, **16**, 4972–4983.
- Fernández-Palacios, J.M., Rijdsdijk, K.F., Norder, S.J., Otto, R., de Nascimento, L., Fernández-Lugo, S., Tjørve, E. & Whittaker, R.J. (2016) Towards a glacial-sensitive model of island biogeography. *Global Ecology and Biogeography*, **25**, 817–830.
- Francalanci, L., Vougioukalakis, G.E., Perini, G. & Manetti, P. (2005) A west-east traverse along the magmatism of the South Aegean Volcanic Arc in the light of volcanological, chemical and isotope data. (ed. by M. Fytikas and G.E. Vougioukalakis), pp. 65–111. *The South Aegean active volcanic arc: present knowledge and future perspectives*. Elsevier, Amsterdam.
- Gouvas, M. & Sakellarios, N. (2011) *Climate and forest vegetation of Greece*, 1st edn. National Observatory of Athens, Athens.
- Greuter, W. (1971) Betrachtungen zur Pflanzengeographie der Südägäis. *Opera Botanica*, **30**, 49–64.
- Greuter, W. (1975) Historical biogeography of the southern half of the Aegean area. *Problems of Balkan flora and vegetation*, pp. 17–21. Publishing House of the Bulgarian Academy of Sciences, Sofia.
- Guimerá, R. & Amaral, L.A.N. (2005) Functional cartography of complex metabolic networks. *Nature*, **433**, 895–900.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Kagiampaki, A., Triantis, K., Vardinoyannis, K. & Mylonas, M. (2011) Factors affecting plant species richness and endemism in the South Aegean (Greece). *Journal of Biological Research*, **16**, 282–295.
- Kallimanis, A.S., Panitsa, M., Bergmeier, E. & Dimopoulos, P. (2011) Examining the relationship between total species richness and single island palaeo- and neo-endemics. *Acta Oecologica*, **37**, 65–70.
- Kapsimalis, V., Pavlopoulos, K., Panagiotopoulos, I., Drakopoulou, P., Vandarakis, D., Sakellariou, D. & Anagnostou, C. (2009) Geoarchaeological challenges in the Kiklades continental shelf (Aegean Sea). *Zeitschrift für Geomorphologie*, **S53**, 169–190.
- Kougioumoutzis, K. & Tiniakou, A. (2014) Ecological factors and plant species diversity in the South Aegean Volcanic Arc and other central Aegean Islands. *Plant Ecology & Diversity*, **8**, 173–186.
- Kougioumoutzis, K., Simaiakis, S.M. & Tiniakou, A. (2014) Network biogeographical analysis of the central Aegean archipelago. *Journal of Biogeography*, **41**, 1848–1858.
- Kreft, H. & Jetz, W. (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, **37**, 2029–2053.
- 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.
- Kuss, S.E. (1975) Die pleistozänen Hirsche der ostmediterränen Inseln Kreta, Kasos, Karpathos und Rhodos (Griechenland). *Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau*, **65**, 25–79.
- Lack, W.H. & Mabberley, D.J. (1999) *The Flora Graeca story*. Sibthorp, Bauer and Hawkins in the Levant. Oxford University Press, Oxford.
- Lumley, T. using Fortran code by Miller, A. (2009) leaps: regression subset selection. R package version 2.9.
- Lymberakis, P. & Poulakakis, N. (2010) Three continents claiming an archipelago: the evolution of Aegean's herpetological Diversity. *Diversity*, **2**, 233–255.
- Manzi, V., Gennari, R., Hilgen, F., Krijgsman, W., Lugli, S., Roveri, M. & Sierro Francisco, J. (2013) Age refinement of the Messinian salinity crisis onset in the Mediterranean. *Terra Nova*, **25**, 315–322.
- Meulenkaamp, J.E., Wortel, W.J.R., van Wamel, W.A., Spakman, W. & Hoogerduyn, S.E. (1988) Hellenic subduction zone and geodynamic evolution of Crete since the late Middle Miocene. *Tectonophysics*, **146**, 203–205.
- Nieto Feliner, G. (2014) Patterns and processes in plant phylogeography in the Mediterranean Basin. A review. *Perspectives in Plant Ecology, Evolution and Systematics*, **16**, 265–278.
- Normand, S., Ricklefs, R.E., Skov, F., Bladt, J., Tackenberg, O. & Svenning, S.-C. (2011) Postglacial migration supplements climate in determining plant species ranges in Europe. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 3644–3653.
- 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.
- Panitsa, M., Trigas, P., Iatrou, G. & Sfenthourakis, S. (2010) Factors affecting plant species richness and endemism on land-bridge islands – an example from the East Aegean archipelago. *Acta Oecologica*, **36**, 431–437.
- Popov, S.V., Rögl, F., Rozanov, A.Y., Steininger, F.F., Shcherba, I.G. & Kováč, M. (2004) Lithological-Paleogeographic maps of Paratethys. 10 Maps. Late Eocene to Pliocene. *Courier Forschungsinstitut Senckenberg*, **250**, 1–46.
- Poulakakis, N., Kapli, P., Lymberakis, P., Trichas, A., Vardinoyannis, K., Sfenthourakis, S. & Mylonas, M. (2014) A review of phylogeographic analyses of animal taxa from

- the Aegean and surrounding regions. *Journal of Zoological Systematics and Evolutionary Research*, **53**, 18–32.
- Proulx, S.R., Promislow, D.E.L. & Philipps, P.C. (2005) Network thinking in ecology and evolution. *Trends in Ecology and Evolution*, **20**, 345–353.
- R Core Team. 2015: R: A language and environment for statistical computing. – Vienna: R Foundation for Statistical Computing. Available at <https://www.R-project.org/>.
- Rangel, T.F., Diniz-Filho, J.A.F. & Bini, L.M. (2010) SAM: a comprehensive application for spatial analysis in macroecology. *Ecography*, **33**, 46–50.
- Rechinger, K.H. (1943) Flora Aegaea. *Akademie der Wissenschaften Wien, Mathematische-Naturwissenschaftliche Klasse Denkschrift*, **105**, 1–924.
- Rechinger, K.H. (1950) Grundzüge der Pflanzenverbreitung in der Aegäis I–III. *Vegetatio*, **2**, 55–119, 239–308, 365–386.
- Rechinger, K.H. & Rechinger-Moser, F. (1951) *Phytogeographia Aegaea*. Akademie der Wissenschaften Wien, Mathematische-Naturwissenschaftliche Klasse, Denkschrift 105. Springer, Wien.
- Rijsdijk, K.F., Hengl, T., Norder, S.J., Otto, R., Emerson, B.C., Ávila, S.P., López, H., van Loon, E.E., Tjørve, E. & Fernández-Palacios, J.M. (2014) Quantifying surface-area changes of volcanic islands driven by Pleistocene sea-level cycles: biogeographical implications for the Macaronesian archipelagos. *Journal of Biogeography*, **41**, 1242–1254.
- Runemark, H. (1970) The plant geography of the central Aegean. *Feddes Repertorium*, **81**, 229–231.
- Sakellariou, D. & Galanidou, N. (2016) Pleistocene submerged landscapes and Palaeolithic archaeology in the tectonically active Aegean region. *Geology and archaeology: submerged landscapes of the continental shelf* (ed. by J. Harff, G. Bailey and F. Lüth), pp. 145–178. Geological Society, Special Publications 411, London.
- Schüle, W. (1993) Mammals, vegetation and the initial human settlement of the Mediterranean islands: a palaeoecological approach. *Journal of Biogeography*, **20**, 399–412.
- Steinbauer, M.J., Field, R., Grytnes, J.A. et al. (2016) Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography*, **25**, 1097–1107.
- Strid, A. (1996) Phytogeographia Aegaea and the Flora Hellenica Database. *Annalen des Naturhistorischen Museums in Wien*, **98**, 279–289.
- Strid, A. (2016) Atlas of the Aegean flora. *Englera*, **33**, 1–1578.
- Strid, A. & Tan, K. (1997) *Flora Hellenica*, Vol. 1. Koeltz Scientific Books, Königstein.
- Triantis, K.A. & Mylonas, M. (2009) Greek islands, biology. *Encyclopedia of islands* (ed. by R. Gillespie and D.A. Glague), pp. 388–392. University of California Press, Berkeley.
- Trigas, P., Panitsa, M. & Tsiftsis, M. (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.
- Turrill, W.B. (1929) *The plant-life of the Balkan Peninsula*. A phytogeographical study. Clarendon Press, Oxford.
- Vilhena, D. & Antonelli, A. (2015) A network approach for identifying and delimiting biogeographical regions. *Nature Communications*, **6**, 6848.
- Weigelt, P. & Kreft, H. (2013) Quantifying island isolation – insights from global patterns of insular plant species richness. *Ecography*, **36**, 417–429.
- Weigelt, P., Steinbauer, M.J., Cabral, J.S. & Kreft, H. (2016) Late Quaternary climate change shapes island biodiversity. *Nature*, **532**, 99–102.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Network analysis – Bibliographical sources.

**Appendix S2** Supplementary analyses, results and figures.

**Appendix S3** Topological linkage values.

## BIOSKETCH

**Kostas Kougioumoutzis** is a post-doc fellow with a keen interest in the island biogeography and plant diversity of the Aegean region.

Author contributions: K.K. and P.T. conceived the ideas; K.K., A.T.V. and P.T. collected the data; K.K., E.G. and S.M.S. analysed the data; K.K., K.A.T. and P.T. led the writing and all authors contributed to the writing process.

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