

Network biogeographical analysis of the central Aegean archipelago

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ABSTRACT

Aim Although the factors shaping plant species richness patterns across the islands of the central Aegean are well known, the processes driving the assembly of these island communities remain unclear. To shed light on these processes, we identified biogeographical modules within the phytogeographical area of the Cyclades and tested for nestedness across the islands.

Location The Cyclades, Greece.

Methods We used a network approach to detect island biogeographical roles and modules, based on a large and detailed database of the Greek endemic plant taxa of the Cyclades, and we tested for nestedness in the island–species matrices.

Results The Cyclades were significantly modular and divided into five biogeographical modules. Three of the modules were significantly nested and two displayed all four possible biogeographical roles (*connectors*, *module hubs*, *network hubs*, *peripherals*). Most of the network's taxa are classified as *peripherals* and widespread endemics.

Main conclusions The borders of the five modules correspond remarkably well to the palaeogeographical and climatic compartmentalization of the Cyclades. The flora of the Cyclades has not yet reached the relaxation phase and the region may act as an ecogeographical filter for the distribution of several plant lineages. Naxos, Milos and Anafi play an important role for the network's connectivity, while at least five adjacent phytogeographical regions affect the distribution patterns of the endemic taxa present in the Cyclades.

Keywords

Colonization routes, connectance, Cyclades, dispersal, ecological network, endemism, island biogeography, modularity, nestedness, palaeogeography.

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INTRODUCTION

The Aegean Sea has long attracted the attention of biogeographers (Turill, 1929; Strid, 1996) because of its high environmental and topographical heterogeneity (Blondel *et al.*, 2010), diversity and endemism (Strid, 1996). The Aegean Sea contains more than 7000 islands and islets (Triantis & Mylonas, 2009) of various sizes. Plant distributional origins are, in general, well known (Strid, 1996) with elements originating from three different biogeographical regions, namely Europe, Asia and Africa (Strid & Tan, 1997).

Turill (1929) was the first botanist to divide Greece into 12 phytogeographical regions, while Rechinger (1943, 1950) laid

the foundations of the prevailing phytogeographical subdivision of the Aegean. Strid (1996), based on Rechinger (1943, 1950), divided Greece into 13 phytogeographical areas. Rechinger & Rechinger-Moser (1951), Runemark (1970) and Greuter (1970, 1971) were the first phytogeographers to address the distributional and floristic problems arising from the palaeogeographical history of the Aegean Sea.

The distributional patterns of plant groups in the Aegean Sea may reflect palaeogeographical patterns or historical events (Comes *et al.*, 2008, and references therein). The effect of vicariance events, restricted gene flow and genetic drift in shaping the distribution of the genetic diversity of the Aegean archipelago's flora has also been examined (i.e. Cellinese *et al.*,

2009). Although the effects of characteristics of eastern (Panitsa *et al.*, 2006, 2010), southern (Kagiampaki *et al.*, 2011) and central Aegean islands (Kougiumoutzis & Tiniakou, 2014) upon total and endemic species richness are now well known, our understanding of the processes driving the assembly of the central Aegean island communities is still far from complete. One approach to advancing our understanding of such processes is to analyse if and how individual islands shape species distributions across an archipelago. The Cyclades offer an excellent setting for the analysis of processes underlying species distribution patterns, owing to their variability in size, palaeogeographical history, geological composition, and topographical and climatic characteristics. The phytogeographical region of the Cyclades (ΚΙΚ hereafter) has long been considered floristically impoverished compared with the other phytogeographical regions of Greece (Phitos *et al.*, 1995). However, in a recent analysis (Kougiumoutzis & Tiniakou, 2014), some areas of the Cyclades emerged as plant diversity hotspots. The Cyclades host 1640 taxa (Tan & Iatrou, 2001), 157 of which are Greek endemics (9.38%) and demonstrate lower than normal endemism in relation to their area (Georgioui & Delipetrou, 2010).

The identification of biogeographical provinces (areas of taxa distribution that have similar characteristics and support different biomes) and their delimitation are important goals within biogeography. Nevertheless, several approaches have been proposed for this task (Hausdorf, 2002; Hausdorf & Hennig, 2003) and these often involve an arbitrary delimitation of boundaries (Hausdorf, 2002). Approaches are needed that identify a limited number of a priori hypotheses concerning the predominant factors shaping provinces and which therefore deliver more objective delineations of biogeographical provinces and the connectivity pathways between them (Moallic *et al.*, 2012). Network analysis is a promising and powerful tool for understanding geographical landscape connectivity (Dos Santos *et al.*, 2008), as it provides a holistic approach (free of a priori dataset assumptions), which is better than classical pairwise interaction analyses for assessing interactions within complex datasets (Proulx *et al.*, 2005). Network topology can be analysed with a range of tools and models developed in network theory, allowing inferences on the past or present dynamic properties of the system (Moallic *et al.*, 2012).

In order to identify biogeographical modules (highly linked subgroups of islands and plant taxa; Carstensen & Olesen, 2009) and the topological position of each island within ΚΙΚ's island-species geographical network, we followed a network analytical approach by applying a module-detecting algorithm (NETCARTO; Guimerá & Amaral, 2005a), used in metabolic (Guimerá & Amaral, 2005a), ecological (Olesen *et al.*, 2007) and biogeographical networks (Carstensen & Olesen, 2009; 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). Moreover, NETCARTO detects fine-grained biogeographical patterns (Carstensen & Olesen, 2009) and identifies the spatial importance of islands beyond the importance based on species richness patterns.

We know of no previous study dealing with the compartmentalization and phytogeography of the Cyclades; thus the aim of the present study was: (1) to identify smaller biogeographical groups of islands and plant taxa closely linked together; and (2) to explore for nestedness in the species-islands matrices analysed.

MATERIALS AND METHODS

Palaeogeographical history of the Cyclades

The Aegean Islands are divided into three groups: those lying on the European shelf off the eastern coast of Greece; those associated with Asia Minor's seaboard; and the Cyclades, which form a central, independent shelf that has been separated from Europe since the middle Pleistocene (Foufopoulos & Ives, 1999). Since the peak of the Wisconsin/Würm glaciation, global sea levels have risen 120–130 m, creating, out of what used to be a continuous land coastal landscape, the present island clusters of the Aegean Sea (Pirazzoli, 1991). Between 350 and 250 ka, the subaerial land was extended, the sea was restricted and almost 50–60% of the present Aegean Sea was land with extensive drainage systems, delta plains and large lakes (Lykousis, 2009). Owing to late Pleistocene sea-level regressions, the gaps between mainland Greece and the Cyclades were reduced in width (Greuter, 1979). During the Last Glacial Maximum (LGM; *c.* 20 ka), the area between Evvia, Attiki and Kea was partly exposed to subaerial conditions, while several palaeolakes existed within its central part (Lykousis, 2009). At that time a single large island (*c.* 7600 km²) existed that included the presently existing islands of Andros, Antiparos, Folegandros, Giaros, Ios, Mykonos, Naxos, Paros, Sikinos, Syros and Tinos. Amorgos, Anafi, Kythnos, Santorini, Serifos and Sifnos, as well as Milos' archipelago, remained detached from each other as well as from mainland Greece and from the 'mega-island' during that time. At *c.* 18 ka Giaros was detached from the 'mega-island', while at *c.* 14 ka Kea was separated from South Evvia and mainland Greece and acquired its present status. At *c.* 12 ka the 'mega-island' was divided into two sectors, the northern and the southern; Andros, Tinos, Syros and Mykonos constituted the former, while the latter was composed of Antiparos, Paros and Naxos, together with Sikinos, Folegandros and Ios. From *c.* 10 to 8 ka, the 'mega-island' continued to disintegrate and the area's morphology started to resemble the present status. To the north, Andros and Tinos formed an island separated from Mykonos and Syros. To the south, Antiparos, Paros and Naxos formed an island separated from Ios, while Folegandros detached from Sikinos. From 8 to 6 ka, Kimolos, Polyaeos and Milos were divided into the present islands and the Cyclades acquired their present status (Kapsimalis *et al.*, 2009).

Data

We compiled a database for the Cyclades comprising updated presence–absence data for island plants, containing 159 Greek endemic taxa and including 22 islands. Most islands are of continental origin, with the exceptions belonging to the South Aegean Volcanic Arc (SAVA) (Fig. 1). We used new recorded data (i.e. Kougioumoutzis *et al.*, 2012) and all the bibliographical resources available for the Cyclades (see Appendix S1 in Supporting Information). The total number of endemics of a single island is the sum of the taxa that have a distribution range restricted to Greece. The status of the endemic taxa is based on Tan & Iatrou (2001) and Georghiou & Delipetrou (2010). We did not include in the analysis the total number of native plant taxa present in our dataset because when dealing with phytogeographical issues in the Aegean only the endemic element, rather than the whole flora, is phytogeographically meaningful and informative, at least for the Aegean area (Greuter, 1975).

Simulated annealing

The presence of a link in the matrix between an island and a plant taxon means that the plant taxon is recorded from that island. An island–plant taxa network was thus constructed

from the presence–absence matrix. The network is bipartite, meaning that species never connect to species, and islands never connect to islands. We used NETCARTO, kindly provided by R. Guimerá (Department of Chemical Engineering, Universitat Rovira i Virgili), which uses an algorithm based on simulated annealing in order to assign all nodes (taxa and islands) to modules (small links of highly linked nodes; Guimerá & Amaral, 2005a,b). If NETCARTO is run repeatedly, the affiliation of nodes to modules has an accuracy of 90% (Guimerá & Amaral, 2005a,b). NETCARTO calculates a modularity index M of the matrix, measuring how clearly delimited the network's modules are. As M approaches one the modules are more distinct, and as it approaches zero the less distinct they are (see Guimerá & Amaral, 2005a, for further explanation). 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.

A topological role was assigned to each node, defined by two parameters: the standardized within-module degree (l) and the among-module connectivity (r) (Guimerá & Amaral, 2005a; Olesen *et al.*, 2007). The mathematical formulas and definition of the parameters are provided in Appendix S1.

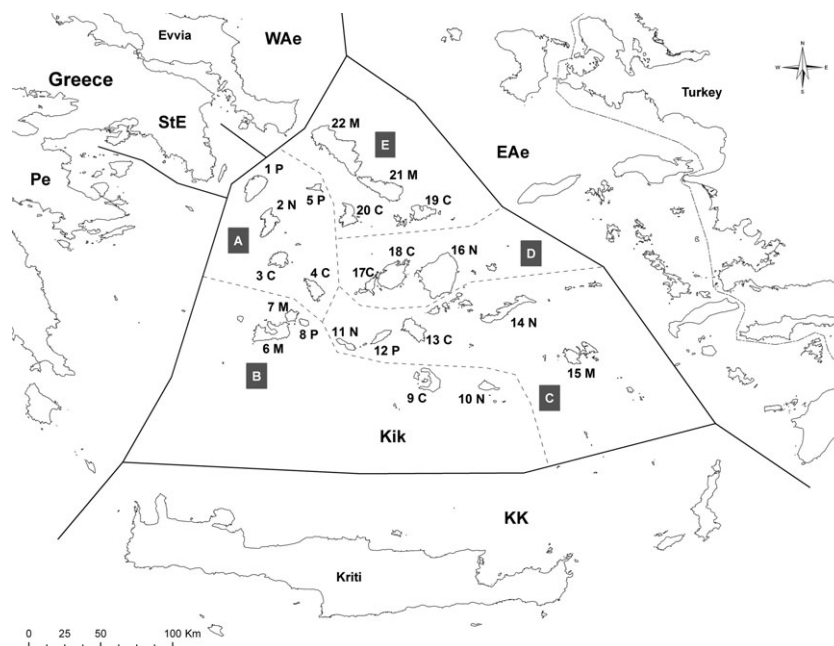


Figure 1 The Cycladic islands included in the present study, as well as the phytogeographical areas encircling that of the Cyclades. Numbers correspond to the islands as follows: 1, Kea; 2, Kythnos; 3, Serifos; 4, Sifnos; 5, Giaros; 6, Milos; 7, Kimolos; 8, Polyaeos; 9, Santorini; 10, Anafi; 11, Folegandros; 12, Sikinos; 13, Ios; 14, Amorgos; 15, Astypalaea; 16, Naxos; 17, Antiparos; 18, Paros; 19, Mykonos; 20, Syros; 21, Tinos; 22, Andros. The phytogeographical regions are abbreviated as follows: East Aegean Islands (E Ae), Cyclades (Kik), Kriti-Karpathos (KK), Peloponnese (Pe), Sterea Ellas (StE) and West Aegean Islands (WAe). C, M, N and P correspond to the island roles: C, *connector*; M, *module hub*; N, *network hub*; P, *peripheral*. A–E indicate the identified biogeographical modules: A, NORTH-WESTERN CYCLADES; B, VOLCANIC CYCLADES; C, SOUTH-CENTRAL & EASTERN CYCLADES; D, PARONAXIA; E, NORTHERN CYCLADES.

We follow Carstensen *et al.*'s (2012) nomenclature regarding l (local topological linkage) and r (regional topological linkage) and the role classification proposed by Guimerá & Amaral (2005a), 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.

In order to measure the structural importance of each node in the network, we used the betweenness centrality index (BCI; Freeman, 1977), calculated by applying Brandes' (2001) algorithm. Betweenness centrality is a measure of the frequency that a node occurs in the geodesic path connecting two other nodes (see Appendix S1 for the mathematical formula and its definition) and determines the relative importance of a node within the network as an intermediary in the flow of information and its vulnerability to fragmentation (Moalic *et al.*, 2012). The network was visualized with GEPHI 0.8.2 beta (Bastian *et al.*, 2009) using the force-based algorithm FORCE-ATLAS (Jacomy, 2009).

Nestedness

Nestedness is a well-known pattern in natural systems where the distribution of organisms is not random. Thus, in true or habitat islands the species comprising smaller local assemblages constitute a subset of the species in richer ones (Patterson & Atmar, 2000). We used ANINHADO (Guimarães & Guimarães, 2006) to estimate the level of the network's nestedness, NODF. If NODF = 100, the matrix is perfectly nested, and if NODF approaches zero, the matrix becomes regular or random. The null model used to assess the significance of NODF (Z -values > 2 indicate significant nestedness at 95% confidence limit) was originally provided by Bascompte *et al.* (2003) and implemented as the C_e model by Guimarães & Guimarães (2006).

In order to unveil the ecological processes that shape the patterns observed in the presence-absence matrix, we used

SDRSIMPLEX (Podani & Schmera, 2011). This method evaluates relativized similarity (S), richness difference (D), species replacement (R), beta diversity ($R + D$), nestedness ($S + D$) and species richness agreement ($S + R$) (see Podani & Schmera, 2011, for more details). The output scores were graphically illustrated by the Ternary Plot option in the NonHier routine of the SYN-TAX 2000 package (Podani, 2001).

RESULTS

Simulated annealing

The island-plant species matrix revealed a significantly modular structure for the total number of endemics ($M = 0.31$, $M_{\text{random}} = 0.30$, $P < 0.05$). Five distinct biogeographical modules were identified (Fig. 1, and Fig. S1 in Appendix S2) and module names are written in small caps as follows. NORTHERN CYCLADES (NC) consists of the highest island in the archipelago, Andros, together with Mykonos, Syros and Tinos. Five islands constitute the SOUTH-CENTRAL & EASTERN CYCLADES (SCEC): Astypalaea, the easternmost island in the archipelago, and Amorgos, Folegandros, Ios and Sikinos. The north-western Cyclades (namely Kea, Kythnos, Serifos and Sifnos), together with Giaros comprise the NORTH-WESTERN CYCLADES (NWC). The islands comprising the VOLCANIC CYCLADES (VC) are all oceanic in origin and constitute the central part of the SAVA; Anafi, Kimolos, Milos, Polyaeos and Santorini belong to this module. Finally, PARONAXIA consists of the largest island in the archipelago, Naxos, as well as Antiparos and Paros. This module and NWC have the largest and smallest species-island ratios, respectively, while NC and SCEC have the largest and smallest percentage of module endemics, respectively (Table 1). Naxos has the highest l and BCI value, while Giaros and Polyaeos have the lowest l and BCI values, respectively (Appendix S2). Two taxa, namely *Galium monachinii* and *Dianthus diffusus*, have by far the largest BCI values (Appendix S2).

Table 1 Description of each biogeographical module in the phylogeographical region of the Cyclades. 'Module endemics' is the percentage of endemic plant taxa designated to a given module that are not distributed on islands outside this module. S_{Wds} , S_{Brg} , S_{Cyc} and S_{SIE} are the number of the widespread (endemic taxa occurring in more than two phylogeographical regions of Greece), biregional (endemic taxa occurring in only two phylogeographical regions of Greece), Cycladian (endemic taxa occurring only in the phylogeographical region of the Cyclades) and single-island endemic (SIE) taxa present in the network's modules, respectively. The percentage of each module's widespread, biregional, Cycladian and single-island endemic taxa is shown within the parentheses.

Module	No. of islands	No. of taxa	Mean number of taxa per island	Module endemics (%)	S_{Wds}	S_{Brg}	S_{Cyc}	S_{SIE}
NORTHERN CYCLADES	4	33	8.25	63.64	19 (57.58)	6 (18.18)	8 (24.24)	5 (15.15)
SOUTH-CENTRAL & EASTERN CYCLADES	5	34	6.80	47.06	18 (52.94)	9 (26.47)	7 (20.59)	5 (14.71)
NORTH-WESTERN CYCLADES	5	22	4.40	27.27	13 (59.09)	4 (18.18)	5 (22.73)	1 (4.55)
VOLCANIC CYCLADES	5	39	7.80	51.28	20 (51.28)	16 (41.03)	3 (7.69)	0 (0.00)
PARONAXIA	3	31	10.33	38.71	12 (38.71)	8 (25.81)	11 (35.48)	5 (16.13)
Total	22	159	7.23	—	82 (51.57)	43 (27.04)	34 (21.38)	16 (10.06)

Most links in the network are among islands in different modules (64.63% of all the links in the network). Thus, mean module and network connectance (as proposed by Olesen *et al.*, 2007), as well as mean betweenness centrality are high (62.60, 25.46 and 58.35, respectively). On average, a module contains 4.40 ± 0.89 islands and 31.80 ± 6.22 taxa with a species–island ratio of 7.23, module endemism of $45.59 \pm 13.63\%$ and module BCI value of 329.36 ± 394.96 .

Five islands are classified as *network hubs* (i.e. with many links to taxa within their module and many links to taxa in other modules): Amorgos, Anafi, Folegandros, Kythnos and Naxos. Five islands are classified as *module hubs* (i.e. with many links to taxa within their module): Andros, Astypalaea, Kimolos, Milos and Tinos. Eight islands are classified as *connectors* (i.e. with a few links to several modules): Antiparos, Ios, Mykonos, Paros, Santorini, Serifos, Sifnos and Syros. Four islands are classified as *peripherals* (i.e. most of their links are within their module): Giaros, Kea, Polyaeos and Sikinos. Two modules, namely SCEC and VC, displayed all four possible roles, constituting two ‘mini’ archipelagos (Figs 1 & 2).

Most of the plant taxa (81.13%) are *peripherals* – 58.14% of these did not have links outside their own module (module endemics, $r = 0$) – while 18.87% are *connectors* (Appendix S2). More than half of the *peripherals* and the *connectors* are widespread endemics (endemic taxa present in more than two phytogeographical regions), nearly one-third are bi-regional endemics (endemic taxa present in only two phytogeographical regions) and the rest are Cycladian endemics (occurring exclusively in KIK) (Appendix S2).

Most of the taxa on NC, NWC, SCEC and VC are widespread endemics, while the opposite is true for PARONAXIA (Table 1). PARONAXIA and VC demonstrate the highest and

lowest percentage of Cycladian endemics among the five modules, respectively (Table 1). Three modules, namely PARONAXIA, NC and SCEC, can be regarded as speciation centres because each of them hosts five single-island endemics (SIE) and displays high proportions of SIE (16.13%, 15.15% and 14.71%, respectively; Appendix S2). Nearly one-third of the network’s taxa (27.04%) are bi-regional endemics (Table 1), most of which originate from the phytogeographical region of Kriti-Karpathos (KK), followed by those originating from the phytogeographical regions of West Aegean Islands (WAE), Peloponnese (PE), East Aegean Islands (EAE), Sterea Ellas (STE) and North Aegean Islands (NAE) in decreasing order (Appendix S2). More than one-third (41.03%) of VC’s taxa are bi-regional endemics (Table 1), originating from five different phytogeographical regions of Greece (Appendix S2); most of them (62.50%), however, originate from KK and PE. Nearly all (88.89%) SCEC’s bi-regional endemics originate from KK, while half of NC’s bi-regional endemics originate from WAE (Appendix S2) and 60% of the bi-regional endemics shared between Evvia Island and KIK are only present in NC (data not shown). The bi-regional endemics of NWC originate from WAE and KK, while PARONAXIA’s bi-regional endemics originate in decreasing order from WAE, EAE, KK and PE (Appendix S2).

Nestedness

Regarding the entire presence–absence matrix, we detected a significant degree of nestedness (NODF = 30.17, $P < 0.001$). Among the five modules identified by NETCARTO, primarily VC (NODF = 53.49, $P < 0.001$) and secondarily SCEC (NODF = 48.57, $P < 0.01$) and NWC (NODF = 49.19, $P < 0.01$) were significantly nested. With regard to NC and PARONAXIA, at a first glance, the endemic plant taxa seem to be randomly distributed and the smaller islands host random subsets of the flora of the larger islands (NODF = 39.10, $P > 0.05$ and NODF = 46.18, $P > 0.05$, respectively; Table 2).

According to the SDRSIMPLEX approach, the dataset has a compartmentalized and structured pattern, demonstrating a transition from high richness differences ($D = 32.21\%$) towards high species replacement ($R = 48.23\%$) with a low degree of similarity ($S = 19.56\%$) (Table 2, and Fig. S2 in Appendix S2). When we analysed the five modules separately, all of them displayed high rates of species spatial turnover and richness difference (Table 2).

DISCUSSION

Simulated annealing

Runemark (1971) first noticed that there might be some degree of compartmentalization in KIK; based on Lund’s Botanical Museum extensive collections, he grouped together the following islands: Andros–Tinos–Mykonos, Kea–Kythnos–Serifos, Paros–Naxos and Sikinos–Folegandros. NETCARTO recognized five modules that partly concur with Runemark’s

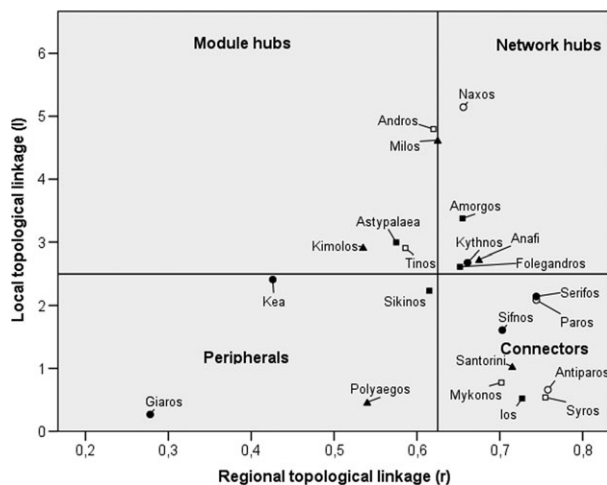


Figure 2 Island role–space for the phytogeographical region of the Cyclades. Open squares indicate the members of NORTHERN CYCLADES, black squares indicate the members of SOUTH-CENTRAL & EASTERN CYCLADES, open circles indicate the members of PARONAXIA, black circles indicate the members of NORTH-WESTERN CYCLADES, and black triangles indicate the members of the VOLCANIC CYCLADES.

Table 2 Summary results of nestedness (NODF) and percentage contributions from the SDRSIMPLEX analyses of the entire network and all detected modules.

Module	NODF	SD	Z-value	S	D	R
Entire Network	30.17**	1.09	7.99	19.56	32.21	48.23
NORTHERN CYCLADES	39.10 ^{n.s.}	4.33	1.23	17.69	47.49	34.82
SOUTH-CENTRAL & EASTERN CYCLADES	48.57*	3.30	2.84	39.34	31.42	29.24
NORTH-WESTERN CYCLADES	49.19*	4.73	2.41	38.19	29.56	32.25
VOLCANIC CYCLADES	53.49**	3.78	3.68	30.32	44.10	25.58
PARONAXIA	46.18 ^{n.s.}	4.85	1.39	31.88	59.37	8.75

NODF, total matrix nestedness; SD, standard deviation; Z-value, [$Z = (\text{observed}(\text{NODF}) - \text{expected}(\text{NODFs})) / \text{standard deviation}(\text{NODFs})$]; S, relativized species similarity; R, relativized species replacement; D, relativized richness difference. * $P < 0.05$; ** $P < 0.001$, n.s.: not statistically significant.

tentative classification. However, Runemark (1971) stated that Serifos and Sifnos, as well as Syros and Tinos show great floristic dissimilarities with each other. In our analysis, these islands were grouped together in the same modules (in NWC and NC, respectively). This difference can be the result of the different techniques used because according to Carstensen & Olesen (2009), a network approach based on simulated annealing is more suitable for detecting fine-grained biogeographical patterns.

The topology derived here shows a striking similarity to the region's palaeogeographical history since the LGM and its evolution over more than 20 kyr. This consistency lends weight to the hypothesis that Quaternary sea-level oscillations, as well as plate tectonic dynamics, may have influenced the current biogeographical structure of the Cyclades (Cellinese *et al.*, 2009, and references therein).

The division of KIK into five clearly defined modules of islands and endemic plant taxa indicates that the region is an agglomerate of smaller areas, reflecting island differences in geological composition, colonization history and speciation, as well as in climatic and topographical characteristics. The borders of the five modules correspond remarkably well with the region's palaeogeographical history and with several ecological gradients (i.e. area, elevation, rainfall), thus highlighting the role of dispersal barriers and colonization routes in delimiting biogeographical modules.

Mean annual precipitation has a strong negative impact on the endemic species richness in KIK and constrains the dispersal of several Greek endemic species in the region (Kougiumoutzis & Tiniakou, 2014). KIK is climatically compartmentalized (Theocharatos, 1978; Koutsoyiannis *et al.*, 2008; Gouvas & Sakellarios, 2011) and the borders of the five modules correspond remarkably well to the climatic compartmentalization of KIK. This finding supports 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 (Kougiumoutzis & Tiniakou, 2014). Our results are also in accordance with the findings of Weigelt & Kreft (2013), who stated that islands receive colonizers from climatically similar areas. Moreover, the western part of KIK has similar climatic characteristics with the north-eastern

part of the Peloponnese (Theocharatos, 1978; Gouvas & Sakellarios, 2011), while NC's climate is similar to that of Evvia. The former situation is reflected by the presence of *Sedum eriocarpum* subsp. *eriocarpum* in Kimolos (a taxon thought to be confined in the Peloponnese; Kougiumoutzis *et al.*, 2014), and the latter by the presence of *Fritillaria erhartii*, *Hypericum delphicum* and *Malcolmia macrocalyx* subsp. *scyria* in Evvia (Trigas, 2003), as well as in Andros (*F. erhartii* occurs also in Syros and Tinos).

The Greek endemic flora has been influenced by an east-to-west migration during the Miocene and by a north-to-south migration in consecutive waves (Iatrou, 1986). Several dispersal events may have occurred as many times as the various continental fragments reconnected to the mainland or to each other as a result of sea-level changes (Cellinese *et al.*, 2009), while some dispersal events from mainland or other continental fragments may have also occurred by island hopping (Lieberman, 2005). This is evident in the composition of the biregional endemics of the five modules (Table 1). As we discuss below (*Differential immigration*), representatives of all the surrounding phytogeographical areas are found in KIK. There is a gradual and sequential change in the representation of biregional endemics along a north-south and an east-west axis, perfectly mirroring the migration waves of the Greek endemic flora, as stated by Iatrou (1986). Thus, biogeographically, the Cyclades may actually function as a dispersal filter between continents, as the Cretan mountains did regarding the southern Aegean endemics (Trigas *et al.*, 2013).

Peripherals and *connector* islands can be interpreted as sink islands, which tend to be small, less mountainous, with low speciation rate and endemism (Carstensen *et al.*, 2012). This is in accordance with our results, because the Cycladic islands classified as *peripherals* are on average smaller, lower and less species-rich than the rest parts of the network (see Appendix S3). On the other hand, *connector* islands can be interpreted as stepping stones for dispersing species (Carstensen *et al.*, 2012). In our network, eight islands were classified as *connectors*. Even though all modules contain *connector* islands, NWC plays the most important role regarding the dispersal of endemic taxa from the mainland (both from SE and PE) to the rest of the Cyclades. This is not unexpected,

taking into consideration the small inter-island distance between the members of this module and the other modules, as well as the small island–mainland distance between the nearest island of this module (Kea) to the mainland (Appendix S3). Islands classified as *network hubs* could act as speciation centres (Carstensen *et al.*, 2012). In our analysis, among the five *network hub* islands, this is true for Amorgos and Naxos, as they host four and five SIE, respectively, and their mountain ranges constitute two of the most important Aegean cliff refugia (Phitos *et al.*, 1995).

Two modules, SCEC and VC, display all four possible island roles, thus acting as archipelagos within the archipelago. This kind of superficial independence is due to the recent and oceanic origin of VC, which differs fundamentally from that of the rest of the Cycladic islands. As for SCEC, it is attributed to the fact that its islands have very strong phytogeographical connections with KK, rather than with any other phytogeographical area surrounding KIK.

VC and NWC are the most and less species-rich modules in the network, respectively (Table 1). This is not surprising because in the Cyclades geologically more diverse islands host higher than average plant diversity and, more specifically, the volcanic islands of KIK demonstrate high plant species richness values (Kougioumoutzis & Tiniakou, 2014). NC has the highest module endemism in the network. This is because its islands have an entirely different climatic regime than the other members of KIK, a factor that affects the Greek endemic taxa's distribution in KIK (Kougioumoutzis & Tiniakou, 2014). Finally, VC do not host any SIE, contrary to the network's other modules. The islands comprising this module have a brief and simple geological history compared with the other Cycladic islands and have experienced a series of mild or even catastrophic (in the case of Santorini) eruptions since their emergence; thus, there was not enough time for species to evolve and diversify in the VC.

Naxos has by far the highest BCI value, followed by Milos and Anafi (Appendix S2). 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, Naxos is the corner-stone for the network's coherence, connecting all the modules together, acting both as a speciation centre and a source island to the other islands in the network. Milos and Anafi, located in the south-western and south-eastern part of KIK, respectively, play a lesser, but equally important role for the network's connectivity because they act as bridges between the rest of the Cycladic islands and PE and KK, respectively.

Nestedness

In natural ecosystems, species assemblages among true islands often show a nested pattern (Lomolino *et al.*, 2006), so that the flora of less diverse (in terms of species richness) islands is a non-random subset of the flora of more diverse islands (Patterson & Atmar, 2000). Recently, Olesen *et al.* (2007) suggested that matrices (with > 150 nodes) may be

both nested and modular. Our matrix had 181 nodes (islands and taxa) and was significantly modular and nested, yet not perfectly ordered. The degree of nestedness was also lower than that reported for terrestrial isopods, land snails (Sfenthourakis *et al.*, 1999), centipedes (Simaiakis & Martínez-Morales, 2010) or land birds (Simaiakis *et al.*, 2012). However, these studies investigated the nestedness patterns of the entire fauna and not those of only the endemic species, which are idiosyncratic, reduce nestedness and result in high local species spatial turnover (Ulrich *et al.*, 2009). There are several reasons why species assemblages may deviate from a nested pattern: increased local speciation, differential or even stochastic immigration and extinction, habitat heterogeneity and peculiarities in local palaeogeography (Wright *et al.*, 1998; Sfenthourakis *et al.*, 1999). In the phytogeographical region of Cyclades, nearly all these factors are present.

Local speciation

High speciation and colonization rate reduce the degree of nestedness (Wright *et al.*, 1998; Sfenthourakis *et al.*, 1999). KIK exhibits high speciation rates, both at the regional and local level (Table 1), because in the Cyclades there has been active differentiation of endemics inside numerous islands (Cardona & Cotandriopoulos, 1978). All five modules have a high degree of Cycladian endemism and four of them host SIE (except VC), with PARONAXIA displaying the highest proportion of Cycladian endemism and SIE. Rare Cycladian endemics and SIE significantly affect nestedness measures (Sfenthourakis *et al.*, 1999; Simaiakis & Martínez-Morales, 2010); in fact, the two modules that did not show significant nestedness were the ones with a higher number of Cycladian endemics and SIE (NC and PARONAXIA).

Differential immigration

The effect of species exchange between any adjacent continental region (serving as a species pool) and the islands tends to weaken the effect of extinction in producing a nested structure (Wright *et al.*, 1998). This is true for the Cyclades because they are surrounded by continental Greece in the west, Anatolian peninsula in the east and Kriti-Karpathos complex in the south.

At least six adjacent phytogeographical regions (EAE, KK, NAE, PE, STE and WAE) contribute with a differential degree to the taxa composition of the Cyclades, as well as to that of the five modules, as exemplified by the biregional endemics' distribution (Appendix S2). The existence of biregional endemics is a good indication of phytogeographical connections between regions (Georghiou & Delipetrou, 2010). KK plays a major role in the immigration process in KIK, followed by WAE, PE, EAE, STE and NAE in decreasing order. None of the five modules depends on only one of the above-mentioned phytogeographical regions to serve as a species pool, thus highlighting the variety of the possible migration

routes. This is perfectly mirrored in the distribution of the biregional endemics of NC and SCEC. The biregional endemics present on NC originate mainly (66.67%) from WAÆ (and more specifically, Evvia), a fact attributed to the close geographical distance between Andros and Evvia (*c.* 4 km), implying that this shallow strait forms a weak phyto-geographical barrier, confirming, in a sense, the findings of Tri-gas *et al.* (2008), who stated that Evvia has strong phyto-geographical affinities with KIK as a whole. On the other hand, the biregional endemics present on the latter originate primarily (88.89%) from KK, because during the Messinian salinity crisis the southern Cyclades and eastern Kriti were in close proximity (Hsü, 1972; see also Fig. 2 in Triantis & Mylonas, 2009), confirming the findings of Greuter (1971, 1975), who stated that the Cardaean endemic element (endemics found exclusively in the Cretan area and the southern and central Cyclades) reflects the situation during the Pleistocene. Finally, VC hosts the most biregional endemics among the five modules and poses as an excellent example regarding the plethora of the migration routes present in the Cyclades, as representatives from nearly all the phyto-geographical areas surrounding the Cyclades are found there; nevertheless, most of the VOLCANIC CYCLADES's biregional endemics (62.50%) originate from KK and PE, reflecting the close palaeogeographical proximity of the islands comprising this module to Kriti and the Peloponnese.

Palaeogeography

The degree and significance of nestedness differed among the five modules (Table 2); the differences in nestedness patterns are consistent with the complex Pleistocene palaeogeographical history of the Cyclades. In systems that have experienced floral relaxation, nestedness is well developed and consequently is typically high in relict floras (Wright *et al.*, 1998). Cycladian endemics, however, are recent and allopatric in origin (*neo-endemics*; see Comes *et al.*, 2008, and references therein). Moreover, several Aegean endemic complexes have differentiated owing to range fragmentation triggered by Plio-/Pleistocene sea-level changes, as well as to subsequent evolution of the fragmented ancestral stock via genetic drift (*non-adaptive radiation*; Bittkau & Comes, 2005, and references therein), while the Cycladian representatives of the *Nigella arvensis* complex have a late Pleistocene origin, congruent with the area's palaeogeography (Comes *et al.*, 2008). Thus, the endemic flora of the Cyclades is not of relict origin, while the islands comprising KIK did not have a common palaeogeographical history (Kapsimalis *et al.*, 2009). Both these suggestions strongly justify the low degree of nestedness observed in the study area.

Compartmentalization

Although KIK has a low degree of nestedness, it has a compartmentalized and structured endemic flora, demonstrating a transition from high richness differences towards high

species replacement with a low degree of similarity (Fig. S2). The compartmentalized and structured pattern is attributed to the effect the different migration routes have on the composition of the modules. Moreover, the floras of both the islands and modules have not yet reached the relaxation phase, explaining the observed high species spatial turnover. This phenomenon is evident in all five modules and is more pronounced in NC and VC. In the former, this is attributed to the recent separation of Andros and Tinos from Evvia (Kapsimalis *et al.*, 2009), while in the latter, this is attributed to the recent formation of the oceanic islands comprising it, as well as to the historical eruptions documented in Santorini and in other members of the SAVA. The high richness differences are attributable to the differences in area, elevation, mean annual precipitation and human population density between the Cycladic islands (Kougiumoutzis & Tiniakou, 2014). Similar richness differences have been observed in EAÆ and KK and have been attributed to topographical/environmental differences (Panitsa *et al.*, 2010; Kagiampaki *et al.*, 2011). Network and nestedness analysis may thus provide insights regarding the processes driving the composition of eastern and southern Aegean island communities and shed light on the role each individual island plays in shaping species distributions across these two phyto-geographical regions.

CONCLUSIONS

Our study confirms the long-standing view that the plant distributional patterns in the Aegean Sea reflect the area's palaeogeographical history. More specifically, the phyto-geographical compartmentalization of the Cyclades bears a striking resemblance to the area's palaeogeographical evolution since the LGM, as well as to the climatic compartmentalization of the Cyclades. The identified borders of the modules may indicate the main borderline for which islands are sinks or stepping stones for migration and colonization from the surrounding continents; thus the absence of several Peloponnese and East Aegean endemics from the Cyclades ('Kyk-ladenfenster'; Rechinger, 1950) can be attributed to the fact that the Cyclades may have acted as an ecogeographical filter for the distribution of several plant lineages.

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SUPPORTING INFORMATION

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

Appendix S1 List of references used to compile our database and mathematical formulas used in the study.

Appendix S2 Topological linkage values for all the islands and plant taxa included in this study, each module's number and percentage of biregional endemics, and supplementary figures.

Appendix S3 Geographical distance matrix for all the islands and modules of the present study.

BIOSKETCHES

Kostas Kougioumoutzis is a PhD candidate with a keen interest in the biogeography and plant diversity of the South Aegean Volcanic Arc and the Aegean Islands.

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Author contributions: K.K. and A.T. conceived the ideas; K.K. and A.T. collected the data; K.K. and S.T. analysed the data; and K.K., S.T. and A.T. led the writing.

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