



# Plant Diversity and Biogeography of the Aegean Archipelago: A New Synthesis

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## ABSTRACT

The Aegean archipelago is one of the largest archipelagos in the world and has long fascinated biogeographers due to its high environmental heterogeneity, complex palaeogeography, high diversity and endemism. In this study, prominence has been given to the plant diversity and biogeography of the Aegean area. After describing the phytogeographical aspects in the Aegean archipelago from the first division in phytogeographical areas, the current widely used subdivisions to the recent aspects of the Aegean phytogeographical classification, a synoptic analysis of the Aegean plant diversity is presented focusing on the Aegean endemics, the range-restricted plant taxa, the single island endemics, the protected plant taxa and the most Critically Endangered ones. Plant diversification and speciation in the Aegean and factors driving them, as revealed by molecular studies, are discussed briefly. The ruderal, alien and invasive plant taxa richness has also been mentioned. Emphasis is also given to small islands and islets plant species diversity. Factors affecting plant species richness in the Aegean, such as the long-lasting human presence, climate, area, elevation, habitat diversity, isolation, geological substrate and structure are discussed on the basis of different biogeographical studies concerning the Aegean area.

## AEGEAN, THE GREAT ARCHIPELAGO IN THE MEDITERRANEAN HOTSPOT

The Mediterranean Basin constitutes the second largest hotspot at global scale and the largest among the world's five Mediterranean-climate regions (Critical Ecosystem Partnership Fund, 2017). The Mediterranean biome, although representing only 2% of the world's surface area, contains 20% of the total plant species richness (Médail & Quézel, 1997) and regarding plant endemism, 10% of the world's plants occur in the Mediterranean region (Blondel, Aronson, Bodiou, & Bœuf, 2010). The European part of the Mediterranean Basin, rich in islands, is one of the world's major centres of plant diversity, as 10% of all known higher plants are found there (Médail & Quézel, 1997). Multiple factors, such as tectonic movement, earthquakes and volcanic activities and the near-desiccation of the sea during the Messinian Salinity Crisis, have created an ensemble of highly heterogeneous



habitats with diverse topographies, soil types and microclimates related to altitude, slope exposure and precipitation (Blondel et al., 2010).

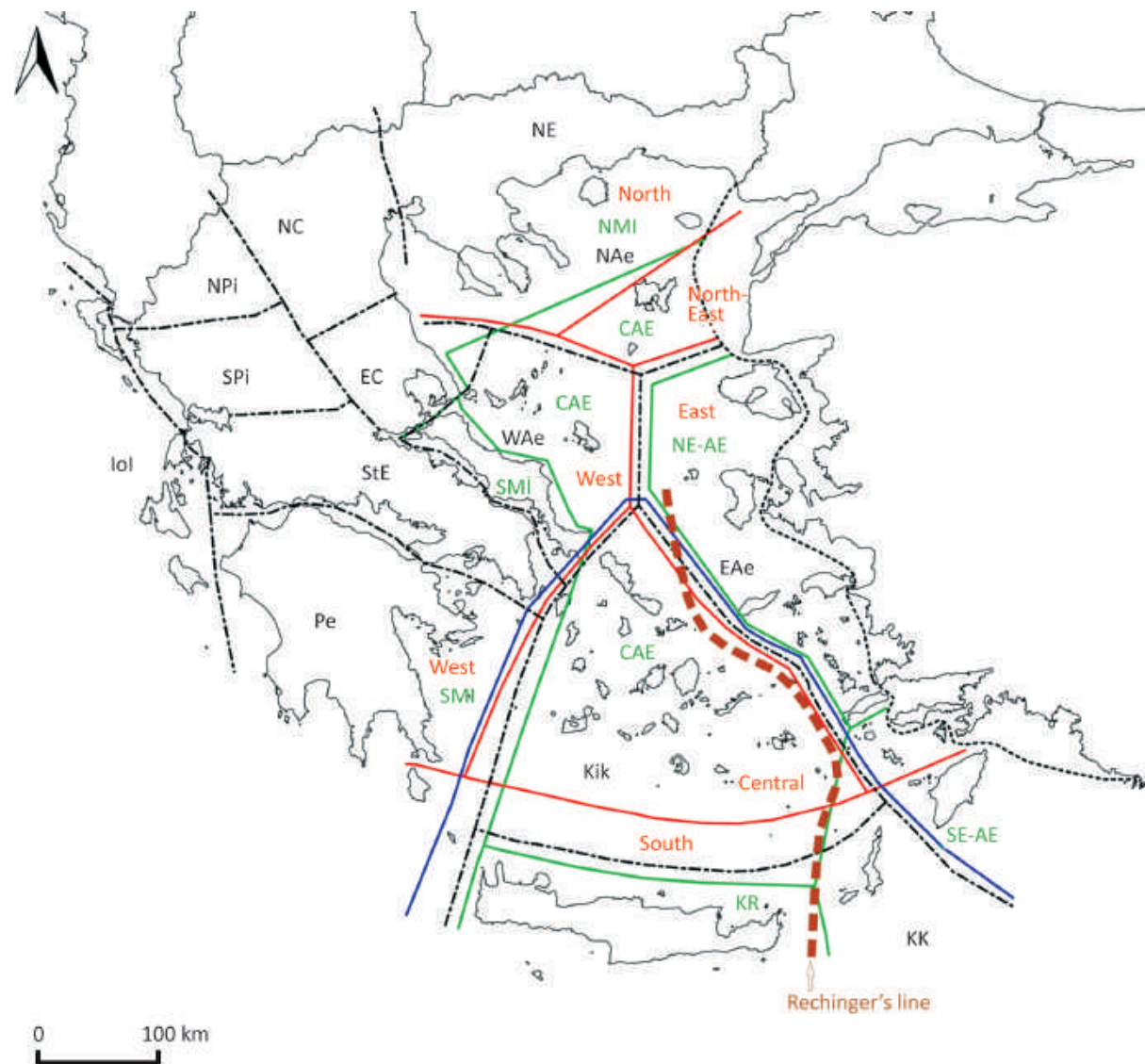
The Mediterranean Basin owes its' topographical complexity largely to the numerous islands that vary in size and are scattered around the Mediterranean Sea. The Aegean Archipelago alone consists of more than 8,000 islands and islets, being one of the largest archipelagos in the world (Triantis & Mylonas, 2009). Every island is unique in terms of geographical and topographical features, e.g., position, size, altitude, geodiversity, origin, geohistorical processes and many more (Tzanoudakis & Panitsa, 1995). Enduring human impact is combined with the geographical features in larger islands to shape the insular flora (Greuter, 1975a, b; Whittaker & Fernández-Palacios, 2007); this is especially true for the Aegean islands, since, nearly 45% of the present Aegean flora has reached the Aegean Islands owing to human action in prehistoric or early historic times (Greuter, 1979).

Crete and southern and central Greece are among the 10 principal plant diversity core areas within the Mediterranean Basin hotspot (Médail & Quézel, 1999). The Aegean Archipelago, lying at the crossroads of three biogeographical regions, namely Europe, Asia and Africa (Triantis & Mylonas, 2009), and constituting a considerable biogeographic barrier between the Balkan and Anatolian Peninsulas, thus triggering the divergence of European and Asian taxa (e.g. Sobierajska et al., 2016; Crowl et al., 2015; Mazur et al., 2018) has long fascinated biogeographers (Turill, 1929), due to its high environmental and topographical heterogeneity, complex palaeogeographical history, as well as high diversity and endemism (Strid, 1996). All the above render it an ideal stage for research in biodiversity, evolution, ecology and biogeographical studies and as such, the Aegean archipelago has the potential to become a model study area globally, especially for land-bridge, continental islands (Sfenthourakis & Triantis, 2017).

Most of the Aegean islands are of continental origin, except those belonging to the South Aegean Volcanic Arc (SAVA), one of the most significant geological structures of the Mediter-

anean, located in the southern Cyclades, as it is found on the edge of two tectonic plates: the African plate and the Aegean-Anatolian microplate (for a thorough review on the SAVA, see Kougioumoutzis & Tiniakou, 2014, and references therein).

The palaeogeographical history of the Aegean is relatively recent and rather complex. The fragmentation of Ägäis (the present-day Aegean, a then continuous large landmass) started during the Middle and Upper Miocene (Creutzburg, 1966; Dermitzakis, 1990). The Aegean's phytogeographical compartmentalization (Figure 1) coincides largely with the Aegean's palaeogeographical history and its evolution during the later stages of the Neogene and the Quaternary. Two main distributional and (palaeo-)geographical barriers exist in the Aegean Archipelago: the Mid Aegean Trench (MAT) and the North Aegean Trench (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, since it distinctively separates Crete from Karpathos, the central Aegean and the Peloponnisos. The MAT does deserve some merit regarding the phytogeographical separation of the central Aegean from the east Aegean, yet its power appears to be diminishing in a S-N axis. 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 impregnable barrier: the North Aegean Islands have very low affinities with the Aegean islands situated south of the NAT. Additionally, the isolation of Crete from Peloponnisos after the Messinian Salinity Crisis and the separation of Karpathos' island group from Rodos in the Pliocene were also very important geological events that created dispersal barriers (Lymberakis & Poulakakis, 2010). Besides, Quaternary sea-level oscillations, as well as plate tectonic dynamics have influenced the current biogeographical structure of the Aegean (e.g. Celli-



**FIGURE 1** ■ Phytogeographical divisions of the Aegean. **Black discontinuous lines** delimit the 13 floristic regions of Greece according to the “Flora Hellenica” project, where the map originates from (Strid, 1996). The Flora Hellenica regions of the Aegean are: **NAe**: North, **WAe**: West, **EAE**: East, **Kik**: Cyclades, **KK**: Crete – Karpathos complex. **Red lines and regions’ names in red** indicate the phytogeographical division by Rechinger and Rechinger-Moser (1951). **Blue lines** delimit Cardaean. **Green lines** are the regions defined by Kougioumoutzis et al. (2017); **NMI**: the northernmost module consisted by the islands of Thasos and Samothraki together with north mainland Greece (NE). **SMI**: Evvoia and the western part of South Aegean island arc are grouped together with the southern parts of mainland Greece. **CAE**: Central Aegean module consisted of the Cyclades together with Northern Sporades and Limnos. **NE-AE**: North-Eastern Aegean module extending from Lesbos to Kos. **SE-AE**: Southeast Aegean module consisted by the complexes of Rodos, Karpathos, Nisyros, Tilos, Symi and Chalki. **KR**: the separated phytogeographical region of Kriti. **Bold red discontinuous line**: Rechinger’s line, generally coinciding with the Mid Aegean Trench (MAT).

nese et al., 2009; Kougioumoutzis, Simaiakis, & Tiniakou, 2014; Simaiakis et al., 2017). Finally, the spatial configuration of the Aegean Archipelago during the last glacial maximum and/or earlier glacials, has had a strong and detectable impact on the plant species' distribution and evolutionary patterns, as in the *Nigella arvensis* complex (Strid, 1970; Comes, Tribsch, & Bittkau, 2008; Comes & Jaros, this volume) and the *Brassica cretica* complex (Edh, Widén, & Ceplitis, 2007). For more information concerning the palaeogeography of the Aegean, see Chapter 1.

The intriguing geological history of the Aegean has been a major factor in the area's phytogeographical patterns creation (e.g. Crowl et al., 2015). During the Pliocene, when the climatic conditions changed from fairly humid to dry, the geographical and/or elevational range of many plant species has changed and there was a spatial isolation among populations located on different areas, resulting in subsequent genetic divergence (Thompson, 2005). Many studies concerning the flora, endemism and phytogeography in the Aegean region have been published (among others, Greuter, 1972, 1975b; Runemark, 1971; Snogerup, 1967; Snogerup & Snogerup, 1987; Carlström, 1987; Strid, 1970, 1972, 1996, 2016a, b; Christodoulakis, 1996; Panitsa, Tzanoudakis, Triantis, & Sfenthourakis, 2006; Panitsa, Tzanoudakis, & Sfenthourakis, 2008, Georgiou & Delipetrou, 2010; Bittkau & Comes, 2005, 2009; Comes et al., 2008; Crowl et al., 2015; Kougioumoutzis, Tiniakou, Georgiou & Georgiadis, 2014, 2015; Kougioumoutzis, et al., 2017; Strid & Tan, 2017) documenting the presence of endemic relict species with a long paleobotanical history and with no close relatives in the current flora as also of endemic species that evolved comparatively recently and chiefly by non-adaptive radiation (Runemark, 1969, 1970, 1971). Evolutionary older plant taxa that already occurred in the Aegean islands they now inhabit long before these became isolated from the adjacent mainland, consist the relict element of the Aegean flora; species that migrated from the adjacent mainland constitute the telechorous or migratory element and species that reached several

Aegean islands due to human-mediated dispersal comprise the anthropophytic element of the Aegean flora (Greuter, 1975a, b, 1979).

## PHYTOGEOGRAPHICAL ASPECTS AND DIVISIONS IN THE AEGEAN ARCHIPELAGO

### First division of the Aegean in phytogeographical areas

The modern botanical exploration of the Aegean Islands dates back to the late 18th century (see Lack & Mabberley, 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. Nearly two decades later, Karl-Heinz Rechinger from the Natural History Museum of Vienna, based on his extensive plant collections during his six field trips in the wider Aegean area between 1927-1942, 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). By combining his own records with those by other botanists, such as Dörfler's from Crete, Hedenborg's from Rodos and Ade's from Tilos and Karpathos, Rechinger published several monumental works: "Flora Aegaea" (Rechinger, 1943a), "Contributions to the Cretan flora" (Rechinger, 1943b) and "Flora Aegaea Supplementum" (Rechinger, 1949), followed by the "Features of plant distribution in the Aegean" (I-III) (Rechinger, 1950).

The criteria which led Rechinger to the imprint of the explicit phytogeographical division of the Aegean had been: i) the distribution range of non-endemic plant taxa, which are restricted to certain parts of the Aegean such as several Anatolian (*Aristolochia hirta*, *Centaurea urvillei*, *Fritillaria bithynica*), North-African (*Medicago heyneana*, *Lycium schweinfurthii*, *Zygophyllum album*) and Balkan elements (e.g. *Paeonia peregrina*), ii) the contrast of some taxa being absent from certain areas, whereas they are widely distributed in other ones (*Kykladenfenster*), iii) the proportion of endemism as a feature of

some parts of the Aegean and iv) the existence of several vicariant taxa (Rechinger, 1943b, 1950; Rechinger & Rechinger-Moser, 1951).

Rechinger's line generally coincides with the Mid Aegean Trench (MAT) and has long been regarded as a very strong biogeographical boundary, largely due to the scarce occurrence of Anatolian floristic elements west of this line. Indeed, for some species complexes (e.g., *Juniperus phoenicea* aggr. and the *Roucela* clade in eastern Mediterranean Campanulaceae), the Aegean Sea separating the Balkan and Anatolian Peninsulas poses as a considerable biogeographical barrier between Europe and Asia acting in a similar way to the Strait of Gibraltar in the western Mediterranean basin, thus triggering the divergence of European and Asian taxa and indicating the important role of the Aegean Sea in the diversification of these closely related taxa (e.g. Sobierajska et al., 2016; Crowlet et al., 2015; Mazur et al., 2018). Nevertheless, Rechinger's line seems to represent a rather weaker than previously thought biogeographical barrier, since the central Aegean acts as a transitional biogeographical zone between Asia and Europe, filtering the distribution of taxa originating from mainland Greece, Anatolia, Crete and the northern Aegean (Kougioumoutzis et al., 2017).

Both Turill and Rechinger noticed the abrupt phytogeographical differences between the Cyclades 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). The consequent phytogeographical regions of the Aegean were:

1. The **West Aegean**, comprising numerous species occurring in mainland Greece; these plant assemblages were an amalgamation of the east Mediterranean, the Balkan and the south European floristic elements.
2. The **North Aegean**, that comprised a zone in which many taxa reached the southernmost limit of their geographical distribution.
3. The **Northeast Aegean**, constituted by taxa of eastern distribution (mostly Anatolian plant taxa).
4. The **East Aegean**, deemed as the phytogeographical border between Europe and Asia, characterized by a large number of Anatolian plant taxa.
5. The **Central Aegean**, viz. the Cyclades island group, which lacks a relatively large number of species otherwise distributed along the rest of the archipelago.
6. The **South Aegean island arc (SAIA)**, constituted an island bridge between mainland Greece and Anatolia. It included Crete, the largest and highest Greek island.

The western and eastern part of SAIA were thought to be more strongly connected – in floristic terms – with the adjacent mainland: the Peloponnisos and Asia Minor, respectively. First and foremost, the Kythira island group is one of the most floristically and phytogeographical intriguing Aegean mini-archipelagos (Tzanoudakis, Panitsa, Trigas, & Iatrou, & 2006); not only it shares several plant taxa with Peloponnisos (Rechinger, 1967; Strid, 1996; Trigas, Tsiptsis, Tsiropidis, & Iatrou, 2012), but also an almost equal number of taxa occur there, as well as in Crete (Rechinger, 1967). Furthermore, Rodos constituted the cornerstone between the phytogeographical regions of South and East Aegean, because it held a dual phytogeographical position between those two regions (Rechinger, 1967).

### Current widely used phytogeographical subdivisions of the Aegean

*Flora Europaea*, based on Rechinger's data, as well as other more recent in-depth studies such as those of Turland, Chilton, and Press (1993), Jahn and Schönfelder (1995), and the *Flora Hellenica* project (Strid & Tan, 1997), consider Crete and the insular complex of Karpathos as a distinctive phytogeographical unit.

Furthermore, a double phytogeographical role is attributed to the central part of the South Aegean Arc, namely Antikythira, Crete and the Karpathos complex by Greuter (1971); Not only they belong to the South Aegean region, but also they are related with Cyclades, all together constituting the part of the Aegean which is phytogeographically more isolated from the continental landmass. Greuter (1971) had named this

region “Cardaean” (“Kardägäis” in German), i.e. “heart of the Aegean”. Runemark (1971) added the island of Ikaria to “Cardaean”. The “Cardaean” is mainly characterized by: (a) a unique endemic element, namely endemics occurring exclusively in the Cretan area and in the southern and central Cyclades (Greuter, 1975b), (b) the lack of species which spread during the Pleistocene, (c) small species numbers except for Crete, (d) a large number of anthropochorous species, and (e) a significant relict element (Greuter, Pleger, & Raus, 1983).

The South Aegean floristic element, correlated to the South Aegean Arc reflects the east to west migration during the Miocene and the “Cardaean” element (the Cretan area and the South and Central Kik) and the palaeogeographical situation during the Pleistocene (Greuter, 1971, 1975b).

In the frame of the *Flora Hellenica* project, Greece was divided in 13 phytogeographical regions (Strid, 1996, Strid & Tan, 1997). Five of these regions (**NAe**: North Aegean, **WAe**: West Aegean, **E Ae**: East Aegean, **Kik**: Central Aegean-Cyclades, and **KK**: Crete-Karpathos) spread in the Aegean archipelago (Figure 1). This subdivision is principally a practical one (Strid, 2000) and it is widely accepted and used in most of the floristic and phytogeographical studies. Especially concerning the Aegean, it also demonstrates phytogeographical borders, based upon Rechinger (1943, 1950), whose aspects proved to be exceptionally precise, even on the basis of contemporary enriched floristic data from the Aegean (Strid, 1996, 2000).

### **Recent aspects of the Aegean phytogeographical classification**

Building upon the aforementioned phytogeographical subdivision, Kougioumoutzis et al. (2017) presented the most recent biogeographical classification of the Aegean archipelago. Via a network optimization approach, six large highly linked subgroups of islands and plant taxa (biogeographical modules) were identified in the Aegean (Figure 1). The northernmost module (**NMI**) consists of Thasos and Samothraki together with north mainland Greece (NE). In

module **SMI**, Evvoia and the western part of South Aegean Arc are grouped together with the southern parts of mainland Greece (Peloponnisos: Pe, and Sterea Hellas: StE). In the Central Aegean module (**CAE**), the Cyclades are grouped together with Northern Sporades and Limnos. North-Eastern Aegean module (**NE-AE**) extends from Lesvos to Kos. The Southeast Aegean module (**SE-AE**) is formed by the complexes of Rodos, Karpathos, Nisyros, Tilos, Symi and Chalki, while Crete is a separated phytogeographical region (**KR**). The delimitation of these six Aegean biogeographical regions is in almost complete harmony with the archipelago’s palaeogeographical evolution from the middle Miocene to the end of the Pleistocene. The biogeographical barriers of the mid-Aegean trench and the North Aegean trench seem to have influenced plant distribution patterns, and the phytogeographical subdivision of the Aegean, both locally and regionally, is similar to the Aegean’s past and contemporary climatic differentiation (Kougioumoutzis et al., 2017).

### **Molecular studies for plant diversification and speciation in the Aegean**

Recent molecular studies (Bittkau & Comes, 2005; Edh et al., 2007) support the theory that plant diversification and speciation in the Aegean region is driven mainly by random (genetic drift) rather than adaptive differentiation among isolated populations (Runemark, 1969; Strid, 1970; Snogerup, Gustafsson, & von Bothmer, 1990; Thompson, 2005). Cellinese et al. (2009) showed that most Cretan *Campanula* species were present in the islands at the time of their isolation, and very little long-distance dispersal to Crete and diversification within Crete has occurred since then. They concluded that endemism is probably driven by loss of species on the mainland after island isolation and that species on the islands may have been more widespread in the past, but they are now restricted to often inaccessible areas, probably as a result of human pressure. Crawl et al. (2015) stated that the evolutionary history and current distributional patterns of endemic *Roucela* complex (Campanulaceae: *Campanula*) are the result of both disper-

sal and vicariance events (through the Miocene and onward) mainly driven by rising sea levels and continental fragmentation. However, Jaros, Tribsch, and Comes (2018) concluded that the MAT does not seem to have played a vicariant role in shaping diversification within *Nigella*, despite its importance as a barrier to dispersal and gene flow in Aegean biota (among others, Runemark, 1980; Crowl et al., 2015; Poulakakis et al., 2014; Sfenthourakis & Triantis, 2017). Hilpold et al. (2014) concluded that there is a clear relation between geography and the structure of the molecular data studying phylogeny of species of the genus *Centaurea*. Kozłowski, Frey, Fazan, Egli et al. (2014) mentioned that relict species provide a unique opportunity to understand past and recent biogeographical and evolutionary processes studying *Zelkova abelicea* (Ulmaceae), one of the most prominent Tertiary relict trees of the Mediterranean region, the only tree endemic to Crete, and promoted the development of new approaches for the improvement of conservation strategies for Tertiary relict trees characterized by major local disjunctions. Bosque et al. (2014) noted that the persistence of the species to climate changes seems to be more complicated and multifactorial than a linear and plain view of species survival in climate refugial areas, and therefore calls for a consideration of the processes in future conservation planning.

Bittkau and Comes (2009), Comes et al. (2008), Jaros et al. (2018), and Comes and Jaros (this volume) emphasized the need to investigate further biological and landscape features and contemporary vs. historical processes in driving population divergence and taxon diversification in Aegean plant radiations.

### Small islands

There is no standard threshold to separate small from large islands. Small islands or islets are usually considered those which are not able to support permanent human activities. According to Greuter (2001) the smallest of the islets should be prioritized in the nature conservation of the Mediterranean Basin. Many studies concerning small islands of the Aegean area have been published (e.g. see Panitsa & Tzanoudakis,

1995 for references; Bergmeier & Dimopoulos, 2001; Bergmeier et al., 2011; Christodoulakis, 2000; Tzanoudakis et al., 2006, Panitsa & Tzanoudakis, 1998, 2001, 2010; Panitsa et al., 2004; Panitsa, Tzanoudakis, Triantis & Sfenthourakis, 2006, 2008; Tzanoudakis et al., 2006; Snogerup & Snogerup, 2004).

Small island floras have special features (Bergmeier & Dimopoulos, 2001). They may include single – islet endemics such as *Anthemis glaberrima* (Rech. f.) Greuter (Greuter, 1968) occurring on Agria Gramvousa, off western Crete, and is considered as a Critical Endangered species, included in Annex II of the Directive 92/43/EC of priority for protection, or *Allium platakisii* Tzanoud. & Kyriot. found on Pontikonisi, an islet between Crete and Antikythira (Tzanoudakis & Kyriotakis, 1993), and others. Small islands also host some taxa shared among them; these are apparently “islet specialist” plant taxa occurring chiefly on islets not more than a few hundred hectares in size (Rechinger & Rechinger-Moser, 1951; Runemark, 1969; Höner & Greuter, 1988; Raus, 1989, 1991; Höner, 1990, Panitsa & Tzanoudakis, 2001; Georgiou, Panitsa, & Tzanoudakis, 2006). Bergmeier and Dimopoulos (2003) discussed the relation between the occurrence and proportion of islet specialist plant taxa and island area, altitude, and grazing. Plant assemblages on these islets can be locally affected by random events and the irregular plant species distribution patterns can be explained by the reproductive drift observed among the populations of taxa on small islands (Runemark, 1969). Non-adaptive radiation is considered the primary evolutionary driver of their small populations (Snogerup, 1967; Runemark, 1970; Strid, 1970).

Additionally, reproductive drift is observed among the populations of taxa on small islands and this phenomenon explains the irregular endemism pattern and the presence/absence pattern of some non-endemic species on small islands (Runemark, 1969).

In most archipelagos, as island size decreases, area gradually becomes inadequate for the estimation of species number (Burns, McHardy, & Pledger, 2009). The phenomenon termed ‘Small Island Effect’, initially mentioned by Pre-

ston (1962), is observed when on islands smaller than an area's threshold value, species richness fluctuates due to factors other than area (e.g. Sfenthourakis, 1996; Whittaker, 1998; Lomolino, 2000; Triantis et al., 2006).

Geophysical traits, such as elevation, islets' shape and degree of isolation, habitat diversity, minimum distance from the nearest species pool and micro-ecological differences, occasional disturbances and other stochastic events, and human interventions, such as grazing and fire, have been considered as factors determining how many and which species are able to maintain their populations on small islands (e.g. Beyhl, 1990; Morrison, 1997, 2002; Bogaert, Salvador-Van, Eysenrode, Impens, & Van Hecke, 2001, Bridges & McClatchey, 2005, Forman, 2006). Species richness on small islands may behave idiosyncratically, but this does not always lead to a typical Small Island Effect (Panitsa et al., 2006). A 'Small Island Effect' was observed in the central, central – eastern and southern part of the Aegean, for islets with an area extent less than 1.165 km<sup>2</sup> for which the species – area relationship was the dominant factor determining species richness but significantly weaker, compared to the respective relationship for larger islands (Kagiampaki, 2011). Minimum distance from the nearest large island and disturbance penetration distance combined with area, managed to slightly increase the percentage of plant species richness explained (Kagiampaki, 2011).

Turnover in time has been examined by Snogerup and Snogerup (1987, 2004) and Panitsa et al. (2008) providing evidence for rapid shifts in species number that may nonetheless be considered as equilibrium dynamics, as islets are able to respond rapidly to environmental

change and disturbance that have a significant complicating effect on community dynamics, enhancing observed turnover rates.

## AEGEAN PLANT DIVERSITY IN GENERAL TERMS – TOTAL PLANT SPECIES RICHNESS

Uotila (2017) showed that the Aegean area belongs to one of the floristically well-mapped areas, mainly within the framework of several detailed projects: i) the *Atlas of the Aegean Flora* (Strid, 2016a, b), ii) the *Annotated Checklist of the Vascular Plants of Greece* (Dimopoulos et al., 2013, 2016), which recorded the distribution of the plant taxa in the 13 floristic regions of Greece, the five floristic regions of the Aegean included, but also iii) *Flora Hellenica* (Strid & Tan, 1997, 2002) and iv) *Atlas Florae Europaea*, a running, long-term program for mapping the distribution of vascular plants in Europe.

Tzanoudakis and Panitsa (1995), Montmollin and Iatrou (1995), Turland et al. (1993), Georghiou and Delipetrou (2010), Kagiampaki (2011), Strid (1996, 2006, 2016), and Strid and Tan (2017) have presented until now the progress in plant taxonomical, floristic and phytogeographical studies concerning Greece or more specifically the Aegean islands and Crete. Since the later publication, eight recently discovered plant taxa (5 species, 2 subspecies and one comb. & stat., have been described from the Aegean area (Kleinsteuber, Ristow, & Hasler, 2016; Galanos & Tzanoudakis, 2017; Trigas, Kalpoutzakis, & Constantinidis, 2017; Rätzel, Ristow, & Uhlich, 2017; Kyriotakis, Antaloudaki, & Tzanoudakis, 2018; Vladimirov, Dane, Matevski, & Tan, 2016; Raab-Straube & Raus, 2017).

**Table 1** ■ Floristic analysis of the 5 Aegean phytogeographical regions. In parentheses, the percentage of the whole Greek flora. Data according to Dimopoulos et al. (2016).

	Families	Genera	Species	Subspecies	Taxa
NAe	145 (78.4)	678 (63.2)	1928 (33.5)	494 (25.1)	1932 (29.2)
WAe	146 (78.9)	695 (64.8)	2024 (35.1)	582 (29.5)	2084 (31.5)
KIK	136 (73.5)	619 (57.7)	1661 (28.8)	458 (23.2)	1750 (26.4)
KK	146 (78.9)	703 (65.5)	2079 (36.1)	571 (29.0)	2214 (33.4)
E Ae	151 (81.6)	756 (70.5)	2381 (41.3)	660 (33.5)	2520 (38.1)



The number of species per surface unit is an important parameter of Aegean vascular plant diversity, regarding the conservation of the diversity of the Aegean area (Panitsa & Tzanoudakis, 2010). Jahn (2003) determined plant species diversity per unit area by subdividing the island of Crete by means of a grid into 343 unit areas (cells) emphasizing that richness in species and endemics are important criteria for plant protection.

### Endemic and range-restricted species richness

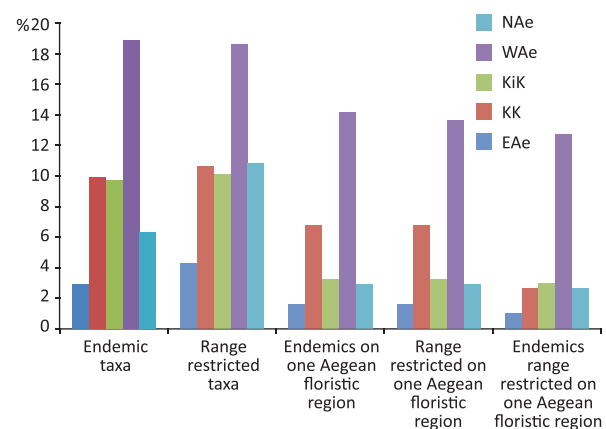
Dimopoulos et al. (2013, 2016) noticed that both the highest and the lowest endemism rate among the Greek floristic regions are within the Aegean area. The highest (17.7%) and lowest (3%) endemism rate is observed in the phytogeographical regions of KK and NAe, respectively. KK hosts 392 Greek endemic taxa. KK is thus the most important endemic hotspot not only in the Aegean region, but in the entire Mediterranean Basin (Médail, 2017).

It should be underlined that the vast majority (62%) of the 740 endemic taxa, are regional endemics (occurring in one of the 5 Aegean floristic regions) while 17.7% are Greek endemics found also on one of the 5 Aegean floristic regions (EAe, WAe, Kik, NAe or KK). Table 3 presents the number of common plant taxa of the whole flora and of the endemic flora among the five Aegean floristic regions. Figure 2 presents the percentages of vascular endemic, and endemic range-restricted plant taxa in each of the Aegean phytogeographical regions of Greece. Figure 3 shows in box plots the Aegean endemic and single island endemic species richness patterns in different phytogeographical areas for islands with large and small size and Figure 4 presents native, Aegean endemic and single island endemic species richness in different phytogeographical areas. When comparing the patterns of endemism and range-restrictedness rates of the Aegean phytogeographical regions, it becomes evident that KK presents a high endemism rate combined with a high rate of range-restrictedness. The phytogeographical region of KK can be regarded not only as a speciation hotspot, but also as the richest island phy-

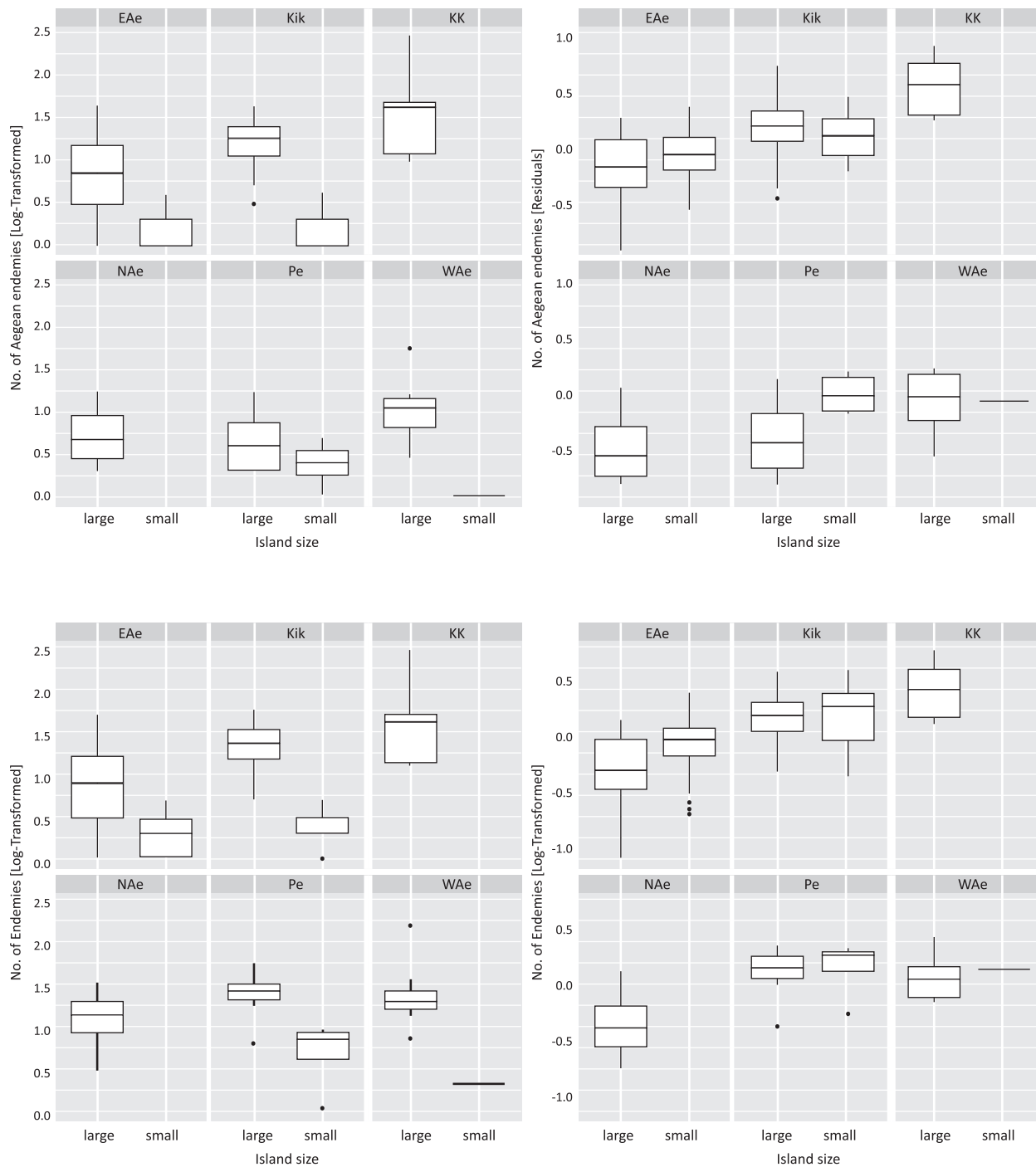
togeographical area in the Aegean in terms of native plant species richness (Figures 3-4). On the other hand, rates of range-restrictedness exceed the respective endemism rates in EAe, WAe and NAe. Moreover, the phytogeographical region of Kik, which has long been held as floristically impoverished (but see Kougioumoutzis & Tiniakou, 2014), emerges as the second richest Aegean phytogeographical region in terms of Greek and Aegean endemic plant species richness and no longer stands out as the poorest Aegean phytogeographical region, regarding native plant species richness, thus confirming the findings by Kougioumoutzis and Tiniakou (2014).

Dimopoulos et al. (2013, 2016) mentioned that range-restricted taxa provide valuable information on the local character, the uniqueness and relations of the Greek and Aegean flora. The Aegean's range-restricted flora consists of 893 taxa, 702 of which are Greek endemics and 577 of these taxa are found only on one of the 5 Aegean phytogeographical regions (Figure 2). Figure 5 presents habitat preferences of the endemic and range-restricted plant taxa of the Aegean area and the differences with the ones of the total Aegean flora.

Most of the endemic and the range-restricted taxa are plants occurring Mediterranean annual-rich grasslands and phrygana grasslands, followed by plants found in grasslands, representing submediterranean/temperate lowland

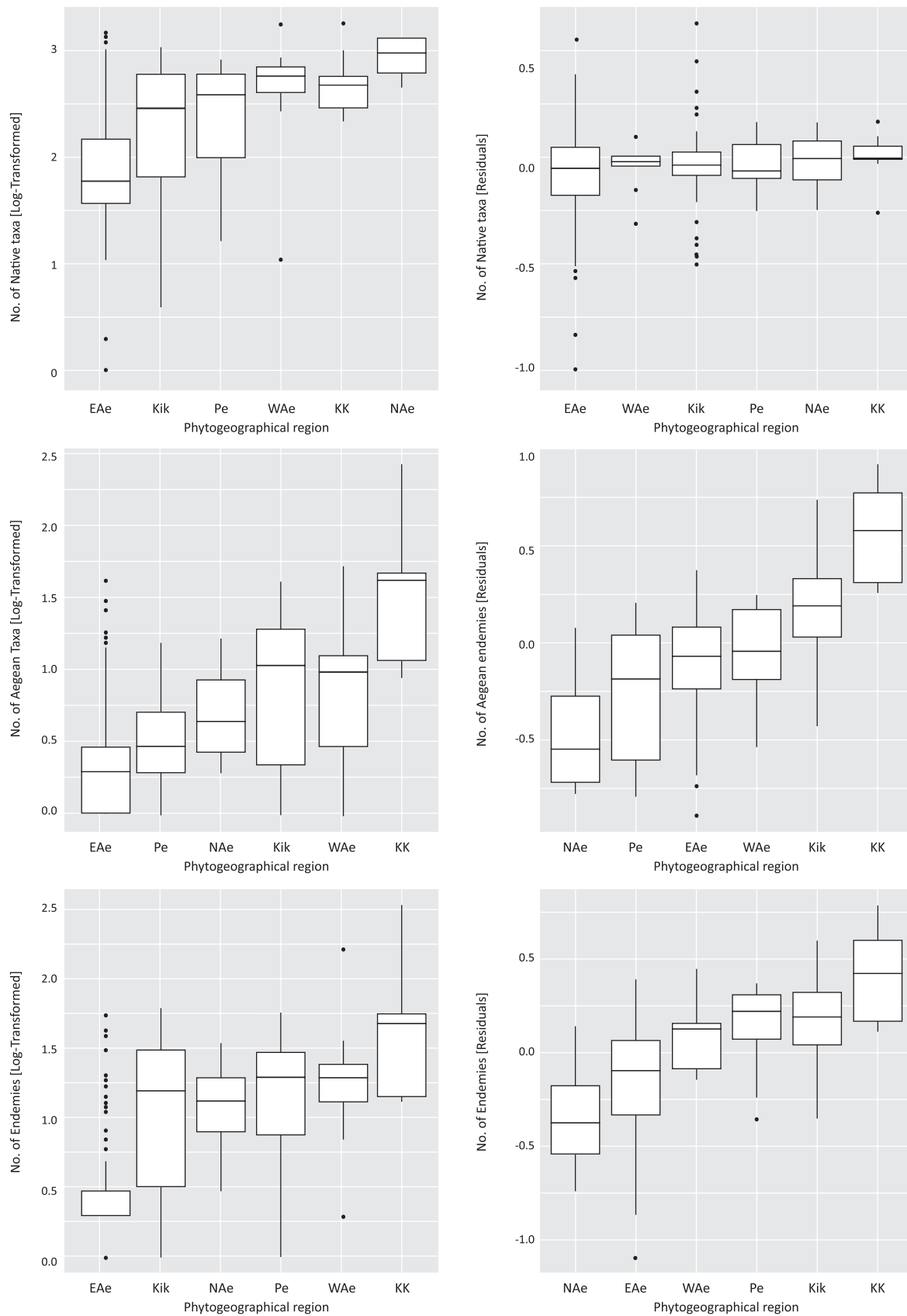


**FIGURE 2** ■ Percentages of vascular endemic, endemic range-restricted and range-restricted plant taxa in each of the 5 Aegean phytogeographical regions of Greece.

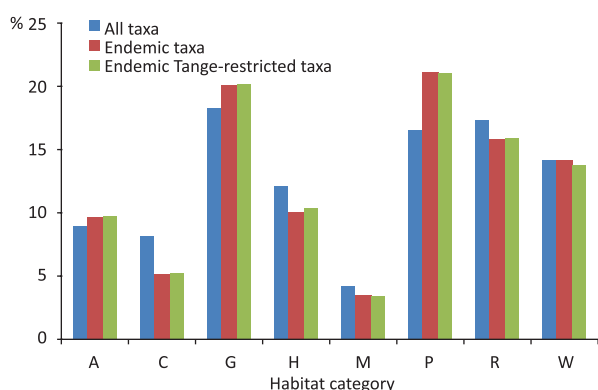


**FIGURE 3** ■ Aegean endemic and single island endemic species patterns in different phytogeographical areas for islands with large and small size.

Plant Diversity and Biogeography of the Aegean Archipelago: A New Synthesis



**FIGURE 4** ■ Native, Aegean endemic and single island endemic species richness in different phytogeographical areas. Abbreviations as in Figure 1.



**FIGURE 5** ■ Habitat categories represented among all taxa, endemic taxa and endemic range-restricted taxa of the Aegean area. Abbreviations as in Dimopoulos et al. (2013, 2016): A: freshwater; C: cliff; G: sub-Mediterranean grassland; H: high mountain; M: coastal/marine; P: Mediterranean grassland and phrygana; R: ruderal and agricultural; W: woodland.

to montane pastures and meadows and then agricultural and ruderal habitats. Specialist plants of high mountains, cliffs, freshwater and coastal habitats, although represented in low proportions, are remarkably prominent in the Aegean flora.

Tzanoudakis et al. (2006) and Panitsa et al. (2004) studied the flora of Antikythira island and the offshore islets of Kythira and Antikythira, and Trigas et al. (2012) showed the conservation importance of Kythira, an island that together with Antikythira and offshore islets, belong to the phylogeographical area of Peloponnisos (PE) and are not included in the five phylogeographical areas of the Aegean.

Some islands like Evvoia and Samos have a dual role, as they not only host many regional endemics, but also numerous Single Island Endemics (SIE) while other islands such as Crete, Karpathos, Naxos, Amorgos, Ikaria and Rodos 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 (Kougioumoutzis et al., 2014, 2017).

A large amount (44.4%) of the plant taxa included in Annexes II, IV & V of the Directive 92/43/EU for the Natura 2000 network are found on the Aegean islands. Some of the most prominent members of this list, are islet specialist plant taxa, such as *Anthemis glaberrima* and *Silene holzmannii*, as well as single island endemic taxa, such as *Bupleurum kakiskalae*.

**Table 2** ■ Endemic and range-restricted plant species richness and rates (in parentheses) of the 5 Aegean phyto-geographical regions. Data according to Dimopoulos et al. (2016).

	Families	Genera	Endemic taxa	Range restricted
All Aegean regions	50	204	740	702
NAe	23	44	57 (3.0)	82 (4.2)
WAe	36	101	102 (4.9)	217 (10.4)
KiK	27	77	162 (9.2)	169 (9.6)
KK	44	160	392 (17.7)	388 (17.5)
E Ae	31	79	152 (6.0)	259 (10.3)

**Table 3** ■ Number of common plant taxa among the Aegean phytogeographical regions. Above the diagonal, numbers of common taxa of the whole flora of the regions, below the diagonal numbers of endemic taxa. On the diagonal, the first number is the endemic taxa and the second is the total taxa per region.

	NAe	WAe	Kik	KK	E Ae
NAe	<b>57</b> 1932	1370	1153	1138	1395
WAe	13	<b>202</b> 2084	1310	1298	1332
KiK	12	42	<b>162</b> 1750	1415	1508
KK	6	29	70	<b>392</b> 2214	1577
E Ae	14	28	52	51	<b>152</b> 2520

Ten of the Top 50 critically endangered Mediterranean Island Plants are hosted on seven Aegean islands, namely, Crete (*Anthemis glaberrima*, *Bupleurum kakiskalae*, *Convolvulus argyrorothamnus* and *Horstrissea dolinicola*), Evvoia (*Allium calamarophilum* and *Minuartia dirphya*), Kythira (*Polygala helenae*), Elafonisos (*Saponaria jagelii*), Samos (*Consolida samia*), Skyros and Skyropoula (*Aethionema retsina*) (Pasta, Perez-Graber, Fazan, & Montmollin, 2017).

Kallimanis, Panitsa, Bergmeier, and Dimopoulos (2011) defined palaeo-endemics as reproductively and geographically isolated species without close relatives and neo-endemics as taxa with many closely related species. They found that palaeo-endemic species richness is correlated only to island area and this is also supported by the presence of palaeo-endemic species only on six of the largest Aegean islands. On the other hand, they showed that neo-endemics as a proportion of the islands flora, is associated only with the islands' maximum elevation and that neo-endemic species richness is also strongly correlated to island area and diversity of geological substrate indicating that an island's habitat heterogeneity is the main environmental driver of speciation.

Dimitrakopoulos, Memtsas, and Troumbis (2004), Trigas, Iatrou, and Karetsos (2007), Panitsa et al. (2010), Iliadou, Kallimanis, Dimopoulos, and Panitsa (2014) found low association between overall species diversity and endemic species richness for Greek as also for Aegean vascular plants. Kallimanis et al. (2010) found that the environmental factors driving total plant species richness and endemic plant species richness differed markedly and that there was a lack of correlation between total species richness and single island endemic (either neo- or palaeo-endemic) diversity as a proportion of the islands flora.

A significant proportion (42.4%) of the endemic taxa occurring in the Aegean archipelago is considered Single Island Endemics (SIE). The vast majority (68.4%) of the Aegean endemics registered on one of the 5 Aegean phytogeographical regions. The island of Crete hosts 61.8% of the SIEs and the island of Evvoia 13.4%. Ikaria, Rodos and Samos host 12 SIEs each, Samothraki 9 and

Thasos 8 SIEs. Kagiampaki, Triantis, Vardinoyannis, and Mylonas (2011) discussed available evidence on local endemics in the South Aegean indicating some cases of in situ speciation like endemic mountain flora of the island of Crete, old relics and SIE. Triantis, Mylonas, and Whittaker (2008) concluded that islands can be considered equivalent to biological provinces for single-island endemics.

### Ruderal plant diversity - Alien and weeds

According to Dimopoulos et al. (2013, 2016) on the five Aegean phytogeographical regions ruderal plant taxa represent 37-41.6% of the total flora, 7.5-13% of which are alien taxa. Concerning their chorology, it is interesting to mention that 1-2.4% are endemics and 1.3-2.7% are range-restricted. Turland, Phitos, Kamari, and Bareka (2004) and Bergmeier (2006) studied the distribution and diversity of plants of traditional agriculture, the weeds of traditional agriculture from Crete (KK), and Bergmeier and Strid (2014) from all over Greece, including information for the five Aegean phytogeographical regions. These authors demonstrated that arable plants reflect phytogeographical and bioclimatic differentiation, in particular along a south-north gradient. Galanos (2015) studied the alien flora of terrestrial and marine ecosystems of Rodos island (EAe).

Gritti, Smith, and Sykes (2006) simulating the vegetation biogeography and dynamics on two of the main islands of the Aegean (Crete and Lesvos) among others, indicated that the effect of climate change alone is likely to be negligible and that the rate of ecosystem disturbance was the main factor controlling susceptibility to invasion, strongly influencing vegetation development on the shorter time scale. Many alien plant assemblages on different islands present an idiosyncratic nature since most alien plants established on Mediterranean islands have the potential to become naturalized on more islands and regional ecological surveys may provide an adequate means to assess this risk (Lloret, Médail, Brundu, & Hulme, 2004; Lloret et al., 2005; Hulme et al., 2008).

## FACTORS AFFECTING PLANT SPECIES RICHNESS

Several researchers have addressed the factors driving the Aegean plant species richness patterns. The most prominent of these factors are discussed below.

### Human presence

Sfenthourakis and Triantis (2017) underlined that the understanding of the interplay between human presence, establishment of exotic species and extinction of indigenous biotas, is of critical importance. Human influence is long-lasting in the Aegean as in the whole Mediterranean area and human factor has significantly shaped the Aegean flora since synanthropic floristic element reaches 30%-50% of some island floras and it is the most effective vector for long-distance dispersal (Greuter, 1975b, 1979, 1995, 2001; Cellinese et al., 2009; Triantis & Mylonas, 2009, Kallimanis et al. 2010, Trigas, Panitsa, & Tsiftsis, 2013). Kougiumoutzis and Tiniakou (2014) suggested that the human factor has played a major role in shaping the pattern observed in the endemic species present in the Cyclades. Stefanaki and Kokkini (2015) noticed that at least some of the rare species recorded exclusively in anthropogenic habitats owe their occurrence there to human activity, and Bergmeier and Strid (2014) determined the distribution patterns and the rarity of many wild plant species of traditional agriculture in Greece revealing the unique character of the east Aegean arable flora. Human presence and the multiplicity of the Aegean geological history are the main factors affecting Aegean island landscapes and their cultural aspects (Panitsa & Dimopoulos, 2015).

### Climate

Climatic differentiations within the Aegean have an impact on both the plant distribution and species richness patterns, as well as on the diversification patterns in the region (Kougiumoutzis et al., 2014; Crawl et al., 2015). Kougiumoutzis et al. (2017) indicated the re-

semblance between the phytogeographical compartmentalization of the Aegean both locally and regionally with the Aegean's past and present climatic compartmentalization and noticed that an island's network position in the Aegean seems to be affected also by contrasting climate regimes and not only by area, elevation and geographical isolation. Iliadou et al. (2014) discussed the effect of the climate concluding that low precipitation and associated summer drought stress in the Aegean might limit the dominance of competitive common species, allowing the persistence of more vulnerable threatened species. Kougiumoutzis and Tiniakou (2014) showed that 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 et al. (2014) also indicated that despite the long recognized floristic impoverishment of the Cyclades islands (Kik), some areas are actually plant diversity hotspots and that there is a phytogeographical compartmentalization within the central Aegean, which reflects two main traits of the area; the palaeogeographical evolution since the Last Glacial Maximum (*ca.* 20 ka), as well as the climatic subdivisions of the same islands. Meusel, Kastner, and Raus (1984) while working in the SE Aegean area on *Carlina tragacanthifolia*, stated that its distribution is explained ecoclimatically by favourable warm winter temperatures and extremely hot summer temperatures in a territory with little rainfall.

Another aspect of the role of the climate as a factor affecting plant species richness in the Aegean is that climate significantly shapes species richness within plant-pollinator communities (Petanidou et al., 2017).

### Area, elevation and habitat diversity

Area and elevation are the major drivers of plant diversity patterns in the Aegean (Panitsa Trigas, Iatrou, & Sfenthourakis, 2010; Kallimanis et al., 2011) and they have a high significance in the differentiation of the Aegean plants (Trigaset al., 2013; Steinbauer et al., 2016; Kou-

gioumoutzis et al. 2014, 2017; Kougioumoutzis & Tiniakou, 2014).

Kagiampaki et al. (2011) provided evidence that species richness and area are strongly related for the South Aegean total vascular species richness, endemism and richness of each plant family. Delipetrou and Georghiou (2010) found that in insular regions there is a predominance of local endemics restricted to or occurring at the thermo-Mediterranean zone, which decreases as the coverage in high mountain sincreases (e.g. KK and NAe).

Concerning the island of Crete, SIE species richness has a unimodal pattern to elevational gradient with a peak at 1,500 m a.s.l. that is holding steady when individual Cretan mountains are considered, indicating that the hump-shaped pattern of SIE is not an artefact of increasing heterogeneity of the SIE species composition with increasing altitude among the Cretan mountains (Trigas et al., 2013). The latter authors however also noticed that subendemic species richness, show a monotonic decrease along the elevation gradient. These results are further supported by endemic species densities along the elevation gradient and they are obviously not affected by taxon-specific traits, since numerous plant families and genera are represented in all endemic species groups averaging taxon-specific patterns.

Panitsa et al. (2010), found that habitat diversity, of which elevation is another dimension, is the main factor affecting floristic richness, total and most of the endemics levels (including single island endemics), on East Aegean islands except the Aegean endemics which are better predicted by elevation. They also noted that elevation can be considered also a dimension of habitat diversity for plants, since higher islands offer a greater variety of habit at types across which endemic plants are not normally distributed.

Cliffs, screes, rocky and other habitats with high stress level are dominated of stress tolerators and correlated to the abundance of endemics (Kypriotakis & Tzanoudakis, 2001; Tzanoudakis et al., 2006; Trigas, Iatrou, & Panitsa, 2008; Panitsa et al., 2010; Panitsa & Kontopanou, 2017, etc.) and this is also the case for

the whole Mediterranean area (Médail & Verlaque, 1997). Cliffs are a conspicuous feature of the Aegean landscape, as also of the Mediterranean, and probably played an important role as a refuge, particularly maritime cliffs and those with a southerly exposure (Thompson, 2005). In cliffs, Thompson (2005) mentioned the fact that obligatory chasmophytes may have persisted alongside with plants characteristic of contemporary garrigues, phrygana, and maquis vegetation during the glacial maxima (Davis, 1951; Snogerup, 1971). On the Cyclades, the present endemic flora grows almost exclusively in habitats that are inaccessible to man and his domestic animals (Snogerup, 1985). This phenomenon according to Runemark (1971) is attributed to the less competitive nature of the endemic Aegean flora against such kind of pressure; most endemic species do not belong to a climax community and do not grow in the habitat which is most suitable for them, but only in habitats where they are permitted to grow by stronger competitors (Runemark, 1971). Rechanger (1965) stated that Aegean endemics are mainly ancient mountain endemics with distribution areas older than the current land/sea distribution, since the present-day Aegean Islands were mountain-tops in the geological past. Indeed, the Aegean limestone cliffs very often harbour endemic taxa (Tzanoudakis et al., 2006). As Snogerup (1995) states, Kalamos Peninsula in Anafi, is among the most important cliff refugia in the Aegean, as more than one-third (37.8%) of the endemic flora of Anafi is located there (Kougioumoutzis, Tiniakou, Georghiou, & Georgiadis, 2012) at elevations below 500 m a.s.l.; including many rare endemic taxa, such as *Campanula laciniata* and *Sternbergia greuteriana*. This phenomenon can be also observed in many other Cycladic Islands, such as Amorgos (Snogerup, 1995).

Legakis and Kypriotakis (1994) concluded that the combination of altitude and climate creates high habitat diversity in Crete, which partly justifies the high endemism on the island and Kagiampaki et al. (2011) showed that habitat diversity alone is sufficient in describing the number of South Aegean endemics.

Topographic and geological heterogeneity

are among the most important factors promoting species richness globally (Whittaker & Fernández-Palacios, 2007; Sfenthourakis & Triantis, 2009) and locally (Kougioumoutzis & Tiniakou, 2014). Sfenthourakis and Panitsa (2011) also showed that diversity at the whole-island scale is shaped mainly by heterogeneity among local communities in small Aegean islands. The *Choros* model (Triantis, Mylonas, Lika, & Vardi-noyannis, 2003) provides about the same prediction of endemics richness as the habitat diversity alone for the east Aegean small islands (Panitsa et al., 2006) but it was most efficient in shaping the number of south Aegean endemics (Kagiampaki et al., 2011).

Trigas et al. (2013) evaluated drivers affecting patterns along the elevational gradient on the island of Crete, focusing on elevation, area, geometric constraints (MDE), Stevens' elevational Rapoport effect and the post-isolation uplift of the Cretan mountains. They concluded that the response of plant species to environmental gradients on continental island systems are determined by a combination of factors, each one with different intensity and duration of influence depending largely on historical parameters.

Panitsa, Koutsias, Tsiripidis, Zotos, and Dimopoulos (2011) describe an integrated GIS-based methodology for conservation value assessment using the traditional species-based and a habitat-based multi-criteria evaluation in 49 small Aegean islands emphasizing the criteria of diversity, rarity, naturalness, replaceability and threat on each habitat type in combination with the number of significant plant taxa. Kagiampaki et al. (2011) examined habitat diversity, based on a transformation of Southern Aegean Indicator Values data (Böhling, Greuter, & Raus, 2002) on light, temperature, moisture and soil salinity, considered some major operative factors which characterize plant habitats.

## Isolation

The labyrinthine palaeogeographical and geological history of the Aegean archipelago has strongly affected plant species distribution patterns (e.g., Kougioumoutzis et al., 2017). On long isolated continental islands like Crete,

mountain isolation is not the main isolating factor. Island isolation is expected to affect endemic species richness, and probably its relationship to altitude, in a rather complex way (Trigas et al., 2013). Kougioumoutzis et al. (2014), through the network biogeographical analysis of the central Aegean archipelago, confirmed the palaeogeographical and climatic compartmentalization of the Cyclades (Kik) and showed that the flora of the Cyclades (Kik) has not yet reached the relaxation phase. This region may act 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 fundamental for both plants and animals in the Aegean corresponding to the palaeogeographical situation during the middle Ionian (Kougioumoutzis et al., 2017). Panitsa et al. (2010) indicated that the occurrence of local endemics might be attributed either to *in situ* speciation in environmentally diverse localities or to the extinction of formerly more widespread species from nearby regions, due to the pronounced and repeated environmental changes during the Pleistocene, to post-glacial human-mediated disturbance, or even to random relaxation processes.

Steinbauer et al. (2016) found an increase in speciation caused by the isolating effect of topography and suggested that the importance of isolation for speciation is consistent with the increase in percent endemism with elevation around the world. Weigelt and Kreft (2013), quantifying island isolation, mentioned that although the distance to the nearest mainland is an adequate and easy-to-calculate measure of isolation, accounting for stepping stones, large islands as source landmasses, climatic similarity and the area of surrounding landmasses increases the explanatory power of isolation for species richness. Relationship of total and endemic plant species richness of the Aegean islands with distance from nearest inhabited island and from nearest mainland have been examined in many studies (e.g. Iliadou et al., 2014; Panitsa et al., 2001, Tzanoudakis et al., 2006; Panitsa & Tzanoudakis 2001, 2010; Kallimanis et al., 2010, 2011; Kagiampaki et al., 2011; Kougioumoutzis & Tiniakou, 2014).



## Geological substrate and structure

Iliadou et al. (2014) stated that the number of Greek endemics and the number of threatened species appear to be strongly correlated to geological diversity in the Aegean islands. Trigas and Iatrou (2006) indicated the strong link of endemic taxa of Evvoia (WAE) to a specific geological substrate (43.6% of the local endemic taxa are exclusively distributed on limestone) and also focused on the isolated serpentine areas of Evvoia which are of special phytogeographical interest, in particular with respect to their position at the southeastern periphery of the whole system of serpentine areas in the Balkans that represent an ancient core of speciation and act likewise as an important refugial habitat for relict elements (Stevanović, Tan, & Petrova, 2007).

Kougioumoutzis and Tiniakou (2014) when studying islands of the SAVA, stated that geodiversity is an important factor in shaping plant species diversity in the Cyclades, while mean annual precipitation, human population density and maximum elevation were significant predictors of the Greek endemics present in the Cyclades.

Dimopoulos, Raus, Mucina, and Tsiripidis (2010) suggested that the formation of local pioneer vegetation on the volcanic islands is not solely controlled by the age of the substrate ('maturation' of the communities through saturation of their local species pools), but it is also under strong control of factors such as the distribution of ashes after the recent volcanic eruptions, and the chemical and physical properties (e.g. nutrient content) of the soils formed by the deposition of the ashes. Karadimou, Kallimanis, Tsiripidis, and Dimopoulos (2015) and Karadimou, Tsiripidis, Kallimanis, Raus, and Dimopoulos (2016) found that different mechanisms play a leading role in community assembly at different scales, studying the mechanisms driving community assembly between volcanic Aegean islands of different age and history of vegetation development and investigating the relationship between trait-based Functional diversity and area, the Functional Diversity - Area Relationship (FDAR) using plant diversity data.

## GENERAL CONCLUSIONS

Studies on biota of the Aegean islands have provided useful insights into several crucial questions in biogeography, ecology and evolutionary biology (Sfenthourakis & Triantis, 2017). The whole Aegean archipelago, characterized as a natural laboratory for biodiversity, biogeography and evolution by many researchers, has a complex geological and palaeogeographical history that varies among its phytogeographical areas, and a different combination of factors of variable intensity and duration time that drives patterns of its impressive plant species richness and endemism. The question concerning factors affecting plant species richness in the Aegean has some answers, also revealed in the present review, showing differences among the different Aegean phytogeographical areas, but the puzzle remains incomplete. Whittaker, Fernández-Palacios, Matthews, Borregaard, and Triantis (2017) suggested that the combination of increasing application of molecular tools with advances in functional trait biology holds promise for unlocking many of the unresolved questions in longer-term (eco-evolutionary) island biogeography.

Additionally, when considering biodiversity conservation (from the species to the ecosystem and landscape levels), island ecosystems, strongly influenced by a diversity of global environmental changes related to land-use practices, climate change, sea level rise, fires and biological invasions, provide significant challenges and offer opportunities for a rapid advance of our understanding on fundamental aspects of human relationships with nature and of conservation strategies (Borges et al. 2018; Medail, 2017; Whittaker et al., 2017; Whittaker & Fernández-Palacios, 2007; Nogué et al., 2017). Since human influence is extremely intense also on Aegean island ecosystems, priority in conservation strategies should be given in education and sensitization of local population to environmental issues and particularly to the special value of Aegean islands as places that house unique components of global biodiversity and, also as crucial parts of our natural and cultural heritage.

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