



Taxonomic and phylogenetic diversity patterns in the Northern Sporades islets complex (West Aegean, Greece)

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Abstract

The Aegean archipelago has long been the main research area of numerous biogeographers, plant ecologists and taxonomists due to its intricate palaeogeography and high environmental and topographical heterogeneity. Nevertheless, some parts of this archipelago are essentially unexplored and the processes driving spatial variation in species composition remain unaddressed. Aiming to fill these gaps, we investigated the flora and plant diversity patterns of the Northern Sporades island group, as well as its biogeographical relationships. The study area lies in the biogeographical region of the West Aegean islands and comprises 23 islands and islets. The total flora of the study area consists of 1202 infrageneric taxa, belonging to 517 genera and 120 families, reflecting its geographical and bioclimatic characteristics. The endemic element consists of 41 taxa (3.4% of the flora), eight of which are restricted to the West Aegean islands and two are single island endemics. Area emerged as the most important variable in shaping plant species richness, while niche-based processes played a lesser role in driving these patterns. Regarding the taxonomic and phylogenetic beta-diversity patterns, environmental filtering and not dispersal limitation seems to shape the plant assemblages of the Northern Sporades islets. Biogeographically, the Northern Sporades island group seems to be closer connected to the Kiklades rather than to Evvia or the adjacent mainland, due to their longer isolation and separate palaeogeographical history during the Quaternary.

Keywords Aegean · Alpha diversity · Beta diversity · Biogeography · Endemism · Environmental filtering

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Introduction

Islands are biodiversity hotspots and regarded as natural laboratories because they provide natural sites for experiments on the processes of island colonization, species turnover (Darwin 1859; Greuter 1995; Denslow 2001) and represent rather simplified real-world systems (Kueffer and Fernández-Palacios 2010). Nevertheless, island insularity differs in intensity, depending on proximity to the mainland (Vogiatzakis et al. 2016) and displays more research advantages compared to the mainland, as ecological and evolutionary processes are relatively easier to detect on islands due to their geographical isolation (Whittaker and Fernández-Palacios 2007). Furthermore, islets are recognized as fragile ecosystems on which random factors, intense environmental variation or human impact can shape the insular flora and vegetation to a great extent, particularly because of the small plant population size (Panitsa et al. 2006).

The Mediterranean Basin, a terrestrial biodiversity hotspot (Médail and Quezel 1997; Myers et al. 2000; Médail

and Myers 2004), is the second largest hotspot in the world (Critical Ecosystem Partnership Fund 2017) and it hosts ca. 10,000 islands and islets. It is characterized by immense biogeographical intricacy (Médail 2017), extremely high diversification rates (Rundel et al. 2016) and high endemism (Rundel et al. 2016), due to its high topographic and climate heterogeneity. Most of these endemics have a very narrow geographical range, often restricted to single islands, mountains or coastal plains, as a result of the region's intricate geography and orography (Rundel et al. 2016 and references therein), thus leading to high taxonomic beta diversity (Thompson 2005). The European part of the Mediterranean alone harbours 10% of all known higher plants (Médail and Quezel 1997). The Aegean archipelago is an important component of the Mediterranean region (Triantis and Mylonas 2009), and its more than 8000 islands and islets, the unique biogeographical position between Africa, Europe and Asia, the high levels of environmental and topographical heterogeneity, and a complex palaeogeographic history contribute to high diversity and endemism (Triantis and Mylonas 2009; Kougiumoutzis et al. 2017), and render it an ideal stage for biodiversity and biogeographical studies (Strid 1996, 2016a, b), especially for land-bridge, continental islands (Panitsa et al. 2018).

Beta diversity compared to alpha diversity, allows testing of different hypotheses about the processes driving species distributions and biodiversity (Valli et al. 2019). In addition, comparison of the taxonomic and phylogenetic beta diversity may reveal the mechanisms that generate and maintain biodiversity, such as geographic isolation, environmental filtering and convergent adaptation (Weinstein et al. 2014). The use of phylogenies is commonly used in community ecology in order to understand the origins and histories of species within a community (i.e. alpha diversity) and explore theories about the influence of historical and ecological factors in structuring communities (Webb et al. 2002; Graham and Fine 2008).

The Aegean archipelago has fascinated many biogeographers, and many studies concerning the flora, endemism and factors affecting plant species richness in the Aegean Sea were conducted (e.g. Panitsa et al. 2006, 2010, 2018; Kallimanis et al. 2010, 2011; Kagiampaki et al. 2011; Iliadou et al. 2014a; Kougiumoutzis and Tiniakou 2014; Kougiumoutzis et al. 2014a, b, 2017). However, most of the biogeographical studies on the Aegean islands have focused on factors influencing plant diversity and endemism, either separately or in comparison with other archipelagos, while there has been limited research on the renewed emphasis on understanding spatial variation in species composition, or beta diversity (Panitsa et al. 2008; Sfenthourakis and Panitsa 2012; Valli et al. 2019). A better understanding of the environmental and geographical drivers that affect beta-diversity patterns and the way that these relationships vary between

regions with different ecological and evolutionary histories may gain insights into the processes of structuring ecological communities (Kraft et al. 2011; Fitzpatrick et al. 2013) and shaping species assemblages on continental island systems (Valli et al. 2019).

However, several factors affecting the diversity and structure of Aegean island plant assemblages have yet to be addressed, such as the phylogenetic aspect of species and beta diversity. By incorporating phylogenetic information in biodiversity and biogeographical studies, the distinct roles of geohistorical and ecological processes in shaping diversity patterns and community structure may be revealed (Webb et al. 2002; Cavender-Bares et al. 2009; Siefert et al. 2013; Swenson 2013; Mazel et al. 2017). Consequently, the evolutionary relatedness of species co-occurring within and across regions can be quantified, and the community phylogenetic structure can then be associated to niche-related, neutral and historical processes that mediate species coexistence (Cavender-Bares et al. 2009; Graham et al. 2009).

The Northern Sporades island complex seems well-suited to better understand the evolutionary and ecological processes that have shaped plant assemblages within the Aegean archipelago, due to the morphology, the geographical isolation, the limited degree of human impact mainly on small islets and the environmental conditions of the Northern Sporades. The vegetation of the islands is mainly composed of evergreen sclerophyllous and phryganic plant communities, while halophytic and chasmophytic communities occur on the coasts and cliffs, respectively.

The main objectives of the present study are to investigate and interpret the (a) taxonomic and phylogenetic alpha and beta-diversity patterns, (b) factors affecting island taxonomic and phylogenetic diversity and (c) the phytogeographical relationships among the studied islets and the Aegean biogeographical regions.

Materials and methods

The Northern Sporades islands and islets complex

The Northern Sporades island group (Fig. 1) belongs to the phytogeographical region of West Aegean Islands sensu Dimopoulos et al. (2013); this is a landmass that separated from the Greek mainland during the Pliocene (Dermitzakis 1990) and according to Sakellariou and Galanidou (2017) it included former peninsulas that were connected to Europe during the Last Glacial Maximum (LGM; ca 21 kyr BP) and had become isolated by sea-level rise. A shallow sea separated the Sporades ridge from the exposed land attached to north-western Anatolia (Sakellariou and Galanidou 2017). The Northern Sporades Archipelago constitutes a series of

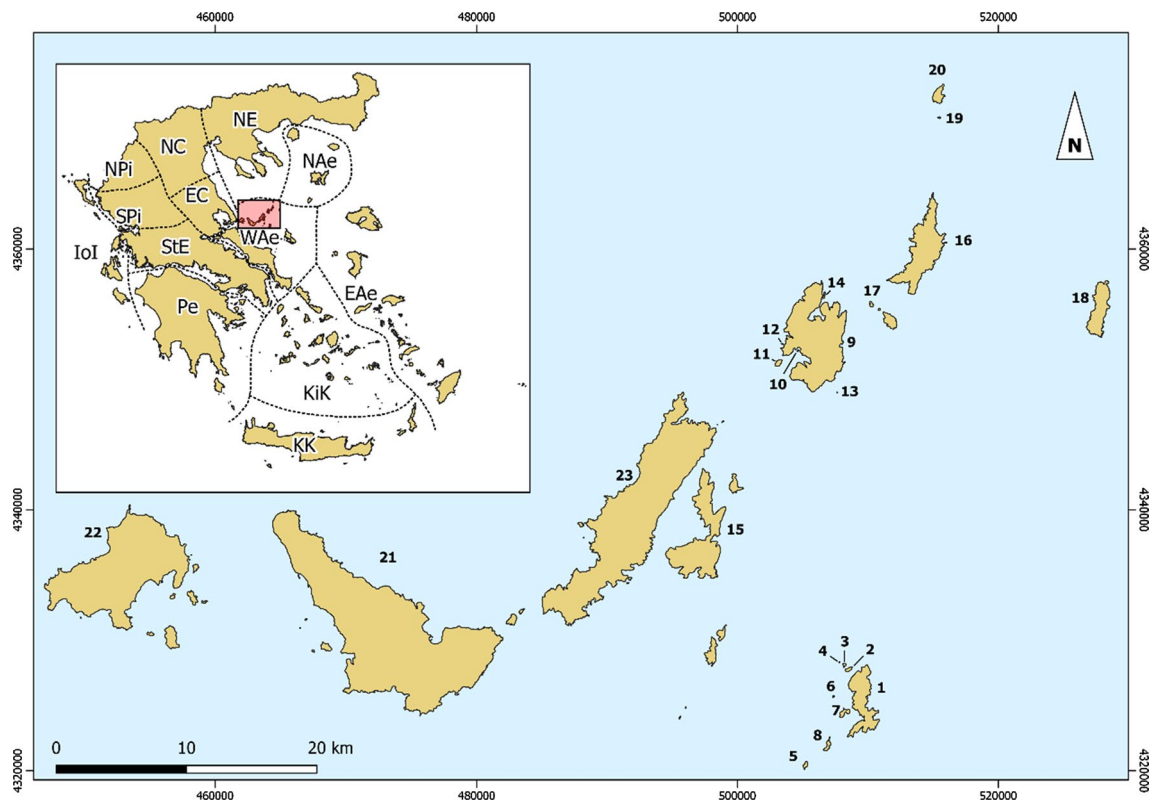


Fig. 1 Map of the Northern Sporades islet complex. Island and islet numbers correspond to the following islands and islets names. 1 Skantzoura; 2 Polemika; 3 Lahanou; 4 Kassidis; 5 Korakas; 6 Stroglylo Skantzouras; 7 Prasso (Paraos); 8 Skantili; 9 Kyra Panagia; 10 Kyra (Ormos); 11 Pelerissa (Fagrou); 12 Pelagonisi; 13 Melissa; 14 Sika; 15 Peristera; 16 Yioura; 17 Pappous; 18 Piperi; 19 Psathonisi; 20 Psathura; 21 Skopelos; 22 Skiathos; 23 Alonnisos. *StE* phytogeographical region of Sterea Ellas; *Pe* phytogeographical region of Peloponnese; *KK* phytogeographical region of Kriti-Karpathos. *EAe*

phytogeographical region of the East Aegean Islands; *Kik* phytogeographical region of the Kiklades; *WAE* phytogeographical region of the West Aegean Islands; *NC* phytogeographical region of North-Central Greece; *SPi* phytogeographical region of South Pindos; *NPi* phytogeographical region of North Pindos; *NE* phytogeographical region of North-East Greece; *EC* phytogeographical region of East-Central Greece; *NAe* phytogeographical region of the North Aegean Islands; *IoI* phytogeographical region of the Ionian Islands

stepping stones between Central Greece and north-western Anatolia (Sakellariou and Galanidou 2017).

Northern Sporades consist of 29 islands and islets of which 22 are uninhabited. Northern Sporades were declared as the first national marine park ‘National Marine Park of Alonnisos and Northern Sporades’ of Greece in 1992 (Presidential Decree 519/28-5-92). Also, it is part of four overlapping NATURA 2000 sites, two Special Areas of Conservation (GR1430004 & GR1430003) and two Special Protection Areas (GR1430005 & GR1430009).

In the present study we focused on 23 islands and islets of the Northern Sporades (Fig. 1, Table 1). The largest island of the study area is Skopelos and the smallest one is Melissa. The highest elevation of the studied islands is the peak ‘Delfoi’ of Skopelos and has a height of 682 m. According to Bornovas and Rondogianni-Tsiambaou (1983), the study area is characterized by nine geological units (Upper Cretaceous limestones, Upper Jurassic limestones, Triassic-Jurassic formations, Flysch, Jurassic schist-chert formations,

Upper Palaeozoic marine deposits, Upper Miocene marine deposits, Holocene alluvial deposits and Mio-Pliocene volcanic rocks). However, most islets are composed of limestones. Except for a part of Kyra Panagia and Piperi that is composed of marine deposits, the largest islands (Skiathos, Skopelos, Alonnisos) are composed of various geological formations. Most islets and islands are hilly with steep cliffs and many caves. All islands are of continental origin as most of the Aegean islands, apart from Psathoura and Psathonisi, which are volcanic in origin.

Only the largest islands (Skiathos, Skopelos, Alonnisos) and Peristera are inhabited. Some of the islets are seasonally or constantly grazed and none is currently cultivated, but relicts of cultivation and human interference were observed. In contrast to Skiathos, Skopelos and Alonnisos that support permanent human population, many villages and agriculture (focused on wine cultivation), grazing, cattle-raising and fishing are the main human activities in the studied N Sporades island complex. During the last years, there have

Table 1 Geographical and ecological information for the Northern Sporades islet complex

Island nr	Island name	Area (km ²)	Elevation (m)	Longitude (E)	Latitude (N)	DM* (km)	Endemic taxa (%)	Total nr of taxa
1	Skantzoura	6.2	107	24.1	39.1	66.3	7 (2.2%)	325
2	Polemika	0.1	40	24.1	39.1	65.2	5 (3.1%)	163
3	Lahanou	0.05	20	24.1	39.1	65	1 (1.5%)	66
4	Kassidis	0.007	1	24.1	39.1	64.6	1 (3.6%)	28
5	Korakas	0.1	16	24.2	39.5	63.6	5 (3.5%)	143
6	Strogylo Skantzouras	0.02	1	24.1	39.1	64.6	1 (1.7%)	60
7	Prasso (Paraos)	0.3	40	24.1	39.1	65.4	8 (4.4%)	181
8	Skantili	0.2	25	24.1	39.0	64.8	9 (5.5%)	165
9	Kyra Panagia	24.8	302	24.1	39.3	61.4	22 (4.1%)	540
10	Kyra (Ormos)	0.009	1	24.1	39.3	62.5	0 (0%)	64
11	Pelerissa (Fagrou)	0.8	60	24.0	39.3	60.6	7 (5.1%)	138
12	Pelagonisi	0.01	1	24.0	39.3	62.1	0 (0%)	26
13	Melissa	0.004	1	24.1	39.3	64.9	1 (4.3%)	23
14	Sfika	0.05	9	24.1	39.4	65.5	3 (5.7%)	53
15	Peristera	14.2	255	24.0	39.2	50.8	7 (2.8%)	252
16	Yioura	11.1	570	24.2	39.4	70.6	27 (5.4%)	500
17	Pappous	0.08	11	24.1	39.4	68.8	2 (2.4%)	83
18	Piperi	4.251	344	24.3	39.4	84.6	7 (4.7%)	149
19	Psathonisi	0.02	2	24.2	39.5	78.5	2 (3.6%)	56
20	Psathura	0.8	12	24.2	39.5	78.9	4 (2.2%)	186
21	Skopelos	95.1	682	23.7	39.1	20.7	16 (2.2%)	742
22	Skiathos	47.4	433	23.5	39.2	4	11 (1.4%)	770
23	Alonnisos	64.1	475	23.9	39.2	41.7	18 (3.0%)	596

DM* minimum distance from nearest mainland coastline

been great tourist pressures as well as various other human interventions. The study area is characterized by a Mediterranean type of climate with wet winters and dry summers, belonging to the subhumid bioclimatic zone characterized by mild winters (Gouvas and Sakellarios 2011). The xerothermic index (Bagnouls and Gaussen 1953) indicates that the study area belongs to the Meso-Mediterranean zone.

Floristic data

We compiled a presence/absence island-plant matrix for the Sporades archipelago, containing 23 islands and islets and 1202 plant taxa (species and subspecies), based on (1) collections and field observations made by Panayotis Dimopoulos (UPA) and Ioannis Bazos (NKUA), who visited the islands together in late April 1999 and April and May 2000, (2) the Atlas of the Aegean Flora (Strid 2016a, b), (3) the Flora Hellenica Database (2019, unpublished data), (4) detailed floristic studies (von Halácsy 1897; Phitos 1967; Economidou 1969, 1973, 1975; Gustafsson and Snogerup 1974; Snogerup et al. 1980, 1991; Liebertz 1981; Kamari et al. 1988; Tsimburla and Yannitsaros 1992; Lowe 1999; Trigas 2003; Biel 2005; Burri and Broggi 2011; Cattaneo and Grano 2012, 2014; Cattaneo et al. 2014), (5) the Atlas of

the Greek Orchids (Antonopoulos and Tsiftsis 2017; Tsiftsis and Antonopoulos 2017) and (6) Sweden's virtual herbarium (2019+). Species nomenclature, life forms, chorological categories and habitat categories follow Dimopoulos et al. (2013, 2016) and their updates included in Dimopoulos et al. (2018). We characterized the occurrence of 'islet specialists' according to Bergmeier and Dimopoulos (2003) and Snogerup and Snogerup (2004). For simplicity, the term "taxa" is used hereafter for both species and subspecies (when a species has more than one subspecies) as in Dimopoulos et al. (2013, 2016).

We estimated the total number of endemics (TE) of a single island as the sum of the taxa with a distribution range restricted to Greece (i.e. Greek endemics). We did not include single island endemics in our analyses, since most of the islands and islets of the Northern Sporades island complex do not host such taxa (except for Skiathos and Piperi). The total number of plant taxa (N) and endemics (TE), as well as the geographical, climatic, and topographical data of the islands and islets of the Northern Sporades island complex are given in Table 1.

Abiotic data

We obtained current climatic data (19 bioclimatic variables) from the WorldClim database (Hijmans et al. 2005) at a 30 s resolution. Soil variables were obtained from the Soil Grids 250 m database (Hengl et al. 2017; <https://www.soilgrids.org>). We used seven soil variables (i.e. pH determined in KCl) that provide predicted values for the surface soil layer at varying depths (0–200 cm). Elevation data were derived from the CGIAR-CSI data-portal (<http://srtm.csi.cgiar.org>—Jarvis et al. 2008) and then were aggregated and resampled using functions from the ‘raster’ 2.6.7 (Hijmans 2017) package, so as to match the resolution of the other environmental variables. We also constructed 16 more climatic variables at the same resolution via the ‘envirem’ 1.1 (Title and Bemmels 2018) package based on the 19 bioclimatic variables from WorldClim. Island area was determined from 1:50,000 scale digital topographical maps obtained from the Hellenic Military Geographical Service (<http://web.gys.gr/GeoSearch/>). Geodiversity was compiled from the 1:500,000 scale Geological Map of Greece (Bornovas and Rondogianni-Tsiambaou 1983).

From this initial set of 45 predictors, only six were not highly correlated (Spearman rank correlation < 0.7 and VIF < 5; Online Resource 1—Rogerson 2001; Dormann et al. 2013). Multicollinearity assessment was performed with the ‘usdm’ 1.1.18 (Naimi et al. 2014) and ‘psych’ 1.8.12 (Revelle 2018) R packages. All analyses and graphs were carried out in the R 3.5.3 (R Development Core Team 2019).

Phylogenetic tree

Since molecular data are not available for many of the plant taxa occurring in the study area, in order to generate a phylogenetic tree we used the GBMB tree (Smith and Brown 2018), i.e. GenBank taxa with a backbone provided by Magallón et al. (2015) that contains 79,874 taxa. We appended any species that were present in our presence/absence matrix, but were missing from the phylogeny by adding them next to a randomly selected congener, following Bruehlheide et al. (2019) and Maitner et al. (2018). We did not add the missing taxa as polytomies to their respective genera, as this approach adds substantial bias to any ensuing analyses (Davies et al. 2012). All analyses and graphs were carried out in the R 3.5.3 (R Development Core Team 2019) using functions from the ‘ape’ 5.3 (Paradis and Schliep 2018) and ‘phangorn’ 2.5.5 (Schliep 2011) R packages.

Land phylogenetic diversity

In order to quantify phylogenetic alpha diversity (PAD) and structure of island floras, we estimated PAD (sensu Faith

1992) of the species inhabiting each of the islands and islets included in the present study with the ‘picante’ 1.6-2 R package (Kembel et al. 2010). We tested for non-random patterns in PAD by estimating their standardized effect size (SES) scores as

$$SES = \frac{X_{obs} - \text{mean}(X_{null})}{\text{s.d.}(X_{null})} \quad (1)$$

where X_{obs} is the observed score within each island and mean (X_{null}) and standard deviation (X_{null}) are the mean and standard deviation of a null distribution of scores generated by shuffling taxa labels of the island-by-species matrix 999 times. We assessed the statistical significance of the SES scores by calculating two-tailed p values (quantiles) as

$$p \text{ values} = \frac{\text{rank}_{obs}}{\text{runs} + 1} \quad (2)$$

where rank_{obs} is the rank of the observed scores compared with those of their null distributions, and runs is the number of randomizations (Kembel et al. 2010). SES scores with $p < 0.05$ and $p > 0.95$ were considered as significantly lower and higher than expected for a given PAD value, respectively. Positive SES values indicate phylogenetic overdispersion, whereas negative SES values indicate phylogenetic clustering. We calculated the standardized effect size scores with the ‘PhyloMeasures’ 2.1 (Tsirogiannis and Sandel 2017) R package. The greater sensitivity of SES_{PAD} to more terminal structure makes it better suited to explore assembly processes working at finer temporal and spatial scales (Mazel et al. 2015).

Regression analysis of alpha diversity

In order to explore the effect of key biological, geographical and climatic variables on species richness of the Sporades archipelago, we modelled the determinants of taxonomic (N and TE) and phylogenetic (PAD_N and PAD_{TE}) island diversity by running a best subset regression analysis (Burnham and Anderson 2002).

A value of 1 was added to TE before \log_{10} -transformation, because zero values were reported for some islands (Brunet and Medellín 2001). Most of the variables had frequency distributions that were strongly positively skewed. Hence, the variables were \log_{10} -transformed to normalize their distribution so that they could be compared with bivariate and multivariate regression methods without heteroscedastic biases and improve the linearity of the relationships in the regression models. A goodness-of-fit test (Shapiro–Wilk and Kolmogorov–Smirnov with 95% level of confidence) to a normal distribution was used to confirm that each transformed variable was successfully transformed to an approximately normal distribution. We compared the models using

R^2 values as a measure of their goodness-of-fit. As the models have the same number of fitted parameters, the R^2 values are directly comparable, without any modification (Triantis et al. 2003, 2005).

We used Akaike's Information Criterion (AIC) to identify the minimum adequate models. This process also allowed calculating the relative importance of each explanatory variable, which captured the percentage of variation explained by each factor when the other factors were held constant. The variance inflator factors (VIF) were below 2.5, thus indicating that multicollinearity was not a problem in any of our obtained models. By fitting the full model, the total adjusted coefficient of multiple determination (R^2_{adj}) was assessed.

All analyses and graphs were carried out in the R 3.5.3 (R Development Core Team 2019) using core functions and functions from the leaps (Lumley 2009) package.

Generalized dissimilarity modelling

We used generalized dissimilarity modelling (GDM; Ferrier et al. 2007) to model pairwise plant community compositional dissimilarity between all the islands and islets included in our analysis as a response to environmental and spatial variables. Taxonomic and phylogenetic beta diversity (TBD and PBD, respectively) and their components were computed using the 'betapart' 1.3 package (Baselga and Orme 2012).

In the GDM framework, a group of curvilinear monotonic functions is used to regress species turnover along environmental gradients, consequently identifying the non-linear relationship between ecological and environmental dissimilarity (Fitzpatrick et al. 2013). The significance of all variables was assessed through a Monte Carlo permutation test (999 repetitions; Manion et al. 2018). Hence, we were able to identify the most significant predictor variables. We extracted for each of these variables the fitted I-spline (a curvilinear line expressing the relationship between species turnover and each predictor—each I-spline has three coefficients). We then plotted the I-splines to investigate the magnitude and rate of beta diversity variation along the most significant predictor variables. We used the sum of the I-spline's coefficients [it defines the proportion of compositional turnover explained by that variable and is determined by the maximum height of its I-spline (Ferrier et al. 2007; Fitzpatrick et al. 2013)] in order to quantify the magnitude of turnover along each gradient. Model fit was assessed via percent deviance explained by the model (Manion et al. 2018). The relative importance of each gradient in driving species turnover was explained as the percent change in deviance explained by the full model and the deviance explained by a model fit with that variable permuted (999 permutations; Manion et al. 2018). All GDM analyses were performed

with the 'gdm' 1.3.7 (Manion et al. 2018) R package in the R 3.5.3 (R Core Development Team 2019).

Phytogeographical relationships

In order to investigate the phytogeographical relationships among the islands and islets constituting the Sporades archipelago, we used the TBD and PBD dissimilarity matrices of their respective turnover component, since it is least affected by variations in species richness (Baselga and Orme 2012), following the framework of Kreft and Jetz (2010). We then applied the unweighted pair-group method using the arithmetic averages (UPGMA) linkage method within a hierarchical clustering scheme, as recommended by Kreft and Jetz (2010). Finally, in order to identify distinct clusters of biogeographical affinities we used the Kelley–Gardner–Sutcliffe (KGS) penalty function, which maximizes differences between groups and cohesiveness within groups based on the respective compositional dissimilarity matrix (Kelley et al. 1996).

Sørensen's index (Sørensen 1948): $C_s = 2j/(a + b)$, where, j = the number of taxa common to both islets, a = the number of taxa recorded from islet 1, b = the number of taxa recorded from islet 2, was used for each pair of islets and islands, to calculate taxonomic similarity between Northern Sporades islands and islets.

Based on a presence/absence matrix of the endemic taxa occurring on the Northern Sporades island complex and the phytogeographical regions of Greece, we carried out a hierarchical cluster analysis in order to measure geographic isolation among floristic regions of Greece. Euclidean distances were computed and the Ward method (Ward 1963) was used to create groups, where the variance within the groups is minimized. The outputs were hierarchical dendrograms, using Statistica software (StatSoft Inc. 2001).

Results

Flora

The vascular flora of the Northern Sporades island complex comprises 1202 taxa (Online Resource 2), belonging to 517 genera and 120 families. Twenty-two taxa are Pteridophytes, six are Gymnosperms and 1174 are Angiosperms (Online Resource 3).

About one-third (31.6%) of the taxa found on the Northern Sporades belong to three families: Fabaceae (136 taxa), Asteraceae (122 taxa) and Poaceae (122 taxa). Also, well represented are the families Brassicaceae (50 taxa), Lamiaceae (49 taxa), Apiaceae (45 taxa), Caryophyllaceae (41 taxa) and Orchidaceae (39 taxa). The most genus-rich families of the Northern Sporades flora are Asteraceae (11.6%

of all genera), followed by Poaceae (10.8% of all genera), Fabaceae and Brassicaceae (6% of all genera).

Therophytes predominate and make up 45.7% of the flora followed by hemicryptophytes and geophytes (Online Resource 3). The Mediterranean chorological category comprises 740 taxa (61.6%); within this group the circum-Mediterranean element predominates (406 taxa), while the East Mediterranean, Mediterranean-SW Asian and Mediterranean-European elements participate in almost equal proportions (8%, 7.8% and 9.4% respectively), highlighting the geographical position and climatic characteristics of the study area. The widely distributed taxa (27.7%) contribute significantly to the flora of the Northern Sporades; the Boreal, European and Circumtemperate elements are represented by few species (Online Resource 3). Balkan taxa are rather few, while the endemics, the most interesting chorological element from a phytogeographical point of view, represent 3.4% of the total flora (41 taxa).

The alien flora of the Northern Sporades comprises 41 taxa (3.4%) belonging to 33 genera and 23 families. The neophytes amount to 78% of the Northern Sporades alien flora (Arianoutsou et al. 2010; Dimopoulos et al. 2013, 2016). On the other hand, 5 alien taxa (*Carpobrotus edulis*, *Morus nigra*, *Paspalum distichum*, *Raphanus sativus* and *Xanthium spinosum*) occur also in small islets of the study area.

Eight islet specialists (*Allium commutatum*, *Anthemis wernerii*, *Atriplex recurva*, *Brassica cretica* subsp. *aegaea*, *Elytrigia sartorii*, *Malva arborea*, *Medicago arborea* and *Trigonella corniculata* subsp. *rechingeri*—Runemark 1969; Snogerup and Snogerup 1987, 2004; Bergmeier and Dimopoulos 2003; Strid 2016a) are present in 22 of 23 islands and islets of the Northern Sporades (except of Kyra Panagia) and are found on cliffs, rocks and coastal habitats (habitat preferences as in Dimopoulos et al. 2013, 2016). More than one-third (37.5%) of the islet specialists are endemic elements and the remaining 62.5% are Mediterranean and East Mediterranean elements.

Endemism

The endemic element consists of 41 taxa making up 3.4% of its total flora, eight of them are endemic to the West Aegean islands and are found on 16 of 23 islets and islands.

The family and genus richest in endemic species are Asteraceae (10 taxa—8.2%—Online Resource 3) and *Campanula* (6 taxa—66.7%), respectively. The most common of them are *Campanula boreosporadum*, *Scutellaria sporadum* and *Campanula scopelia*. Alonnisos, Yioura (6 WAe endemics, respectively) and Kyra Panagia (5 WAe endemics) are the islands richest in WAe endemics. Moreover, two single island endemics exist in the Northern Sporades, *Campanula sciathia* and *Campanula rechingeri* found on Skiathos and Piperi, respectively.

More than two third (Online Resource 3; 73.1%) of the endemic flora are chamaephytes and hemicryptophytes and the endemism of the islets and islands ranges from 0 to 5.7% (Table 1).

Nearly one-third of the endemic taxa (36.6%) found on the Northern Sporades correspond to one or two phytogeographical areas. Seven of 33 endemic taxa (21.2%) are biregional endemics, most of them originating from the phytogeographical region of the Kiklades (Kik—*Campanula reiseri*, *Erysimum senoneri* subsp. *senoneri* and *Fritillaria ehrhartii*) and the East Aegean Islands (EAe—*Centaurea rechingeri* and *Linum gyaricum* subsp. *gyaricum*) followed by those originating from the phytogeographical regions of the North Aegean Islands (NAe—*Malcolmia macrocalyx* subsp. *macrocalyx*) and East-Central Greece (EC—*Verbascum aphentulium*).

Phylogenetic tree

A phylogenetic tree was generated for the 1202 native plant taxa based on the recently published phylogeny of seed plants by Smith and Brown (2018—Online Resource 4). Only 72 taxa (5.99%) could not be added in the GMBM tree, which was subsequently pruned, to contain only the native taxa present in the Sporades archipelago.

Island taxonomic and phylogenetic diversity

Most of the Sporades island floras show a tendency towards phylogenetic clustering (56.5% and 87% for the endemic and native plant communities, respectively; most communities were non-significantly clustered or over-dispersed; Online Resource 1). Four and five endemic and native island plant assemblages, respectively, showed significant phylogenetic clustering ($SES \leq -1.96$ and $p > 0.95$), while only one native island plant community (Skiathos) was significantly phylogenetically over-dispersed ($SES \geq 1.96$ and $p < 0.05$).

Area (A), Thornthwaite aridity index (AIT) and pH were retained in the optimal model for N, while A together with AIT, annual potential evapotranspiration (PET) and precipitation seasonality (PS) were retained in the optimal model for TE (Table 2). As for both the phylogenetic diversity metrics, all six independent variables were retained in the optimal models (Table 2). Area emerged as the most important predictor for both the taxonomic diversity metrics, while climate factors and more specifically, PS and PET, were the main drivers of the endemic and native phylogenetic diversity, respectively (Table 2).

Generalized dissimilarity modelling

The GDM models explained 35.6–62.1% of deviance. (Lower values were observed for PBD than for

Table 2 Summary statistics for predictive models of N, TE, PAD_N and PAD_{TE}, regarding alpha diversity with A, AIT, PET, pH, PS and PWM as proposed by the best subset regression

	Est.	T	<i>p</i>	<i>p</i> _{Bon}	AIC	<i>R</i> ² _{adj}	<i>r</i> _w	<i>F</i>	<i>p</i> value
<i>N</i>					− 18.9	0.91	—	71.9	< 0.001
Intercept	25.28	2.34	—	—			—		
A	0.32	14.45	0.00	0.00			97.07		
pH	− 2.21	− 1.55	0.14	0.41			1.41		
AIT	− 11.31	− 2.07	0.05	0.16			1.52		
TE					7.17	0.81	—	24.6	< 0.001
Intercept	41.83	2.80	—	—			—		
PS	2.26	1.06	0.31	1.00			4.53		
PET	− 5.36	− 1.85	0.08	0.32			2.65		
AIT	− 15.39	− 2.12	0.048	0.19			3.40		
A	0.29	9.42	0.00	0.00			89.43		
PAD _N					68.7	0.69	—	9.31	< 0.001
Intercept	− 805.41	− 4.05	—	—			—		
PWM	90.38	2.69	0.02	0.12			7.91		
PS	− 15.14	− 1.01	0.33	1.00			21.34		
PET	115.80	4.55	0.00	0.00			46.84		
AIT	158.38	3.75	0.00	0.00			9.66		
pH	19.34	1.57	0.14	0.84			8.74		
A	− 0.66	− 3.52	0.00	0.00			5.51		
PAD _{TE}					52.8	0.46	—	4.16	< 0.05
Intercept	− 139.18	− 0.99	—	—			—		
PWM	26.32	1.11	0.28	1.00			4.56		
PS	35.21	3.32	0.00	0.00			37.28		
PET	35.38	1.97	0.07	0.42			7.43		
AIT	− 47.91	− 1.61	0.13	0.78			15.38		
pH	13.47	1.55	0.14	0.84			6.85		
A	− 0.30	− 2.28	0.04	0.24			28.50		

All independent variables and TE were log₁₀-transformed. The adjusted *R*² (total variance explained by each model-*R*²_{adj}), the *p* value, Akaike's Information Criterion (AIC), the estimate (Est.), the significance (*p*), the Bonferroni-corrected *p* values (*p*_{Bon}), as well as the relative importance (*r*_w) of each significant predictor of the best subset regression are reported. A area (km²); AIT Thornthwaite aridity index; PET annual potential evapotranspiration (mm/year); PS precipitation seasonality; PWM precipitation of the year's wettest quarter. pH soil pH; N total number of plant taxa; TE total number of Greek endemic plant taxa; PAD_N island phylogenetic alpha diversity of the native plant taxa; PAD_{TE} island phylogenetic alpha diversity of the Greek endemic plant taxa

Table 3 Deviance explained for the phylogenetic and taxonomic beta-diversity patterns of the native and endemic plant taxa occurring on the 23 islands considered

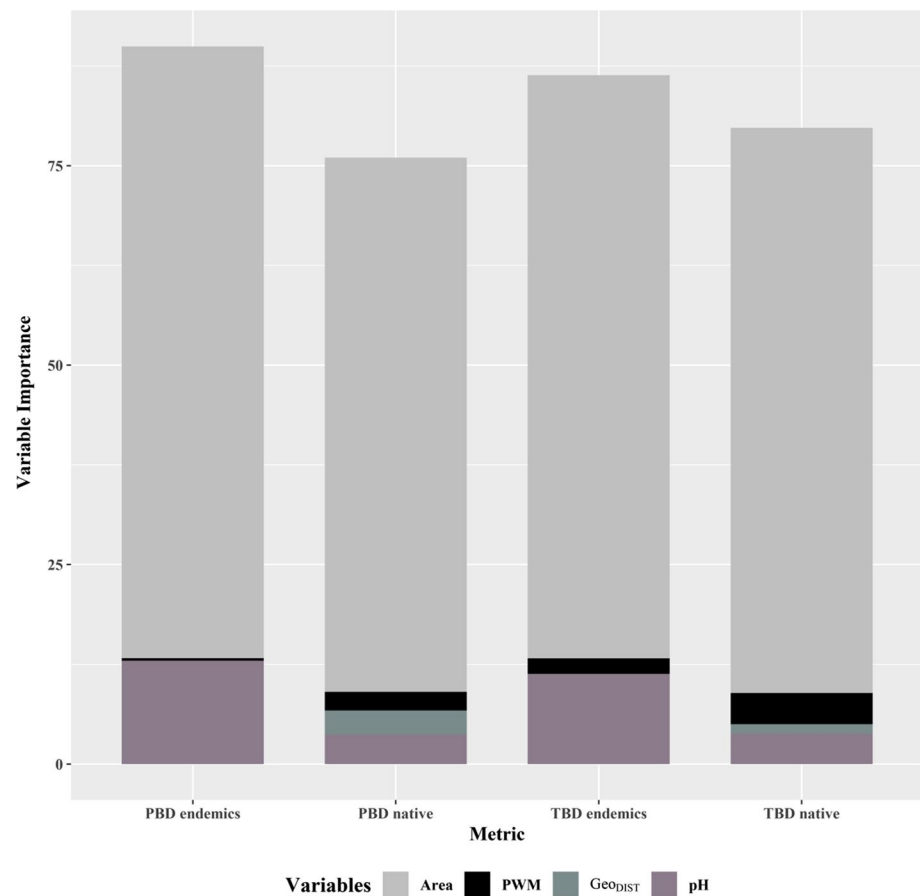
Metric	Taxa	% Deviance explained
TBD	Native	62.1
	Endemic	45.8
PBD	Native	62.0
	Endemic	35.6

PBD phylogenetic beta diversity; TBD taxonomic beta diversity

TBD—Table 3) The most important gradient for all metrics was area, followed by pH (Figs. 2, 3, 4). Geography explained a small fraction of the deviance for all diversity metrics (Fig. 3).

The fitted functions describing the turnover rate and magnitude along each gradient were nonlinear; the turnover rate varied with position along gradients and was greatest at the high and low end of the pH and area gradient, respectively (Fig. 4). More specifically, the island plant communities differed significantly even at areas ca. 1 km² and their composition continued to change with a rapid, but less abrupt trend until the 25 km² threshold (Fig. 4). Soil and climate factors had a more profound effect on the endemic plant communities, which was more pronounced in TBD rather than PBD (Fig. 4).

Fig. 2 The relative importance of each predictor variable in driving beta diversity. *Geo_{DIST}* Geographical distance between the islands; *PWM* precipitation of the year's wettest quarter; *PBD* phylogenetic beta diversity; *TBD* taxonomic beta diversity



Phytogeographical relationships

The floristic relationships between the islets studied expressed by Sørensen's index revealed that the individual islet floras differ from each other from 15.8 to 97.1%.

The floristic independence of the islets and their floristic diversity are illustrated by the fact that 28.6% of the taxa occur on only one of the 23 studied islets and islands. None of the taxa was common to 23 islets and islands, while only 10 taxa (0.8%) were found on at least 19 islets and islands.

Among the islets and islands of the Northern Sporades, hierarchical cluster analysis based on the taxonomic diversity (Online Resource 3) and phylogenetic diversity of Greek endemic taxa (Online Resource 3) show different levels of clustering and divided them into 5 and 4 distinct groups, respectively.

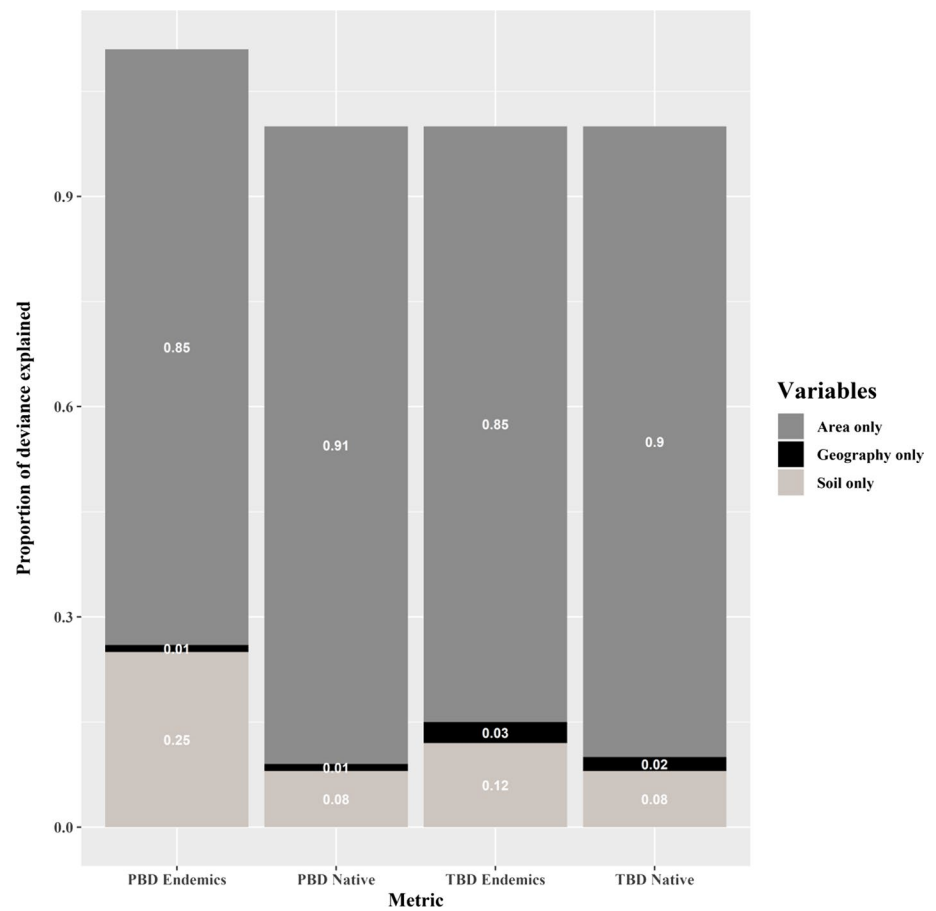
Hierarchical cluster analysis (Fig. 5) revealed that West Aegean Islands (WAe) were clearly clustered with Kiklades (KiK) and East Aegean islands (EAe) and are distant from the other floristic regions based on the distribution of the Greek endemic taxa.

Discussion

Flora

Fabaceae, Asteraceae and Poaceae comprise nearly one-third of the taxa occurring in the Northern Sporades island complex and are among those best-adapted to the ecological conditions of the Mediterranean area as is confirmed by many floristic studies on Greek islands (e.g. Panitsa et al. 2003; Kougiumoutzis et al. 2012a; Iliadou et al. 2014a, b). The high percentage of therophytes (45.7%; Online Resource 3) in conjunction with the high percentage of Mediterranean (61.6%; Online Resource 3) and leguminous taxa (11.3%) reflect the Mediterranean character of the Northern Sporades flora, indicating human-induced disturbances, like grazing and cattle, in Mediterranean ecosystems (Panitsa et al. 2003; Kougiumoutzis et al. 2014b). At present, the natural ecosystems of the Northern Sporades are not endangered by the invasion of alien taxa (3.4%; Online Resource 3) which range below the percentage recorded for the entire Greek flora (c. 5% according to Arianoutsou et al. 2010; c. 3.8%

Fig. 3 The proportion of total deviance explained attributable purely to area (grey), purely to geography (black) and purely to soil (beige) for each beta-diversity metric. *PBD* phylogenetic beta diversity; *TBD* taxonomic beta diversity



according to Dimopoulos et al. 2013, 2016). The vast majority (87.8%) of the alien taxa are found only on the 3 largest, inhabited islands of Skiathos, Skopelos and Alonnisos that are most affected by human impact (tourism, grazing, fires, cultivation, etc.).

The islet specialists, known from various archipelagos around the world, occur mainly on small, low, uninhabited islets exclusively on cliffs, rocks and coastal habitats. The ‘islet phenomenon’ was first described from the Aegean, where the islet specialists constitute a characteristic phytogeographical element (Rechinger and Rechinger-Moser 1951). The islet specialists occur on 22 of the 23 islands and islets of the Northern Sporades (Online Resource 5), their distribution is restricted to the Aegean floristic regions (Runemark 1969; Snogerup and Snogerup 1987, 2004; Bergmeier and Dimopoulos 2003) and they play an important role in the floristic composition of islet vegetation (Panitsa and Tzanoudakis 2010) as a consequence of reduced competition among species, founder and isolation effects, and random eliminations by reproductive drift (Runemark 1969; Bergmeier and Dimopoulos 2003).

Endemism

The patterns of plant endemism richness we observed in Northern Sporades are similar to those occurring in Greece in general (Georghiou and Delipetrou 2010; Dimopoulos et al. 2013, 2016), at the family and genus level. Most of the endemic taxa present in the study area are chamaephytes and hemicryptophytes, scattered mainly in the numerous steep cliffs, rocks and coastal habitats, which very often harbour endemic taxa (Kypriotakis and Tzanoudakis 2001; Trigas et al. 2008; Panitsa and Kontopanou 2017).

The endemism rate of the Northern Sporades (3.4%) is relatively low compared to the total endemic flora of West Aegean islands (c. 9.5% according to Dimopoulos et al. 2013, 2016). However, the endemism rate of WAE is due to the inclusion of Evvia. Evvia is the second-richest Aegean island in terms of single island endemics (40 taxa), is characterized by three centres of endemism (the serpentine regions of N Evvia, Mt Dirphis and Mt Ochi) and hosts 175 Greek endemic elements (Trigas and Iatrou 2006; Trigas et al. 2008). Moreover, the long-lasting separation of Evvia from the Northern Sporades (Sakellariou and Galanidou 2016),

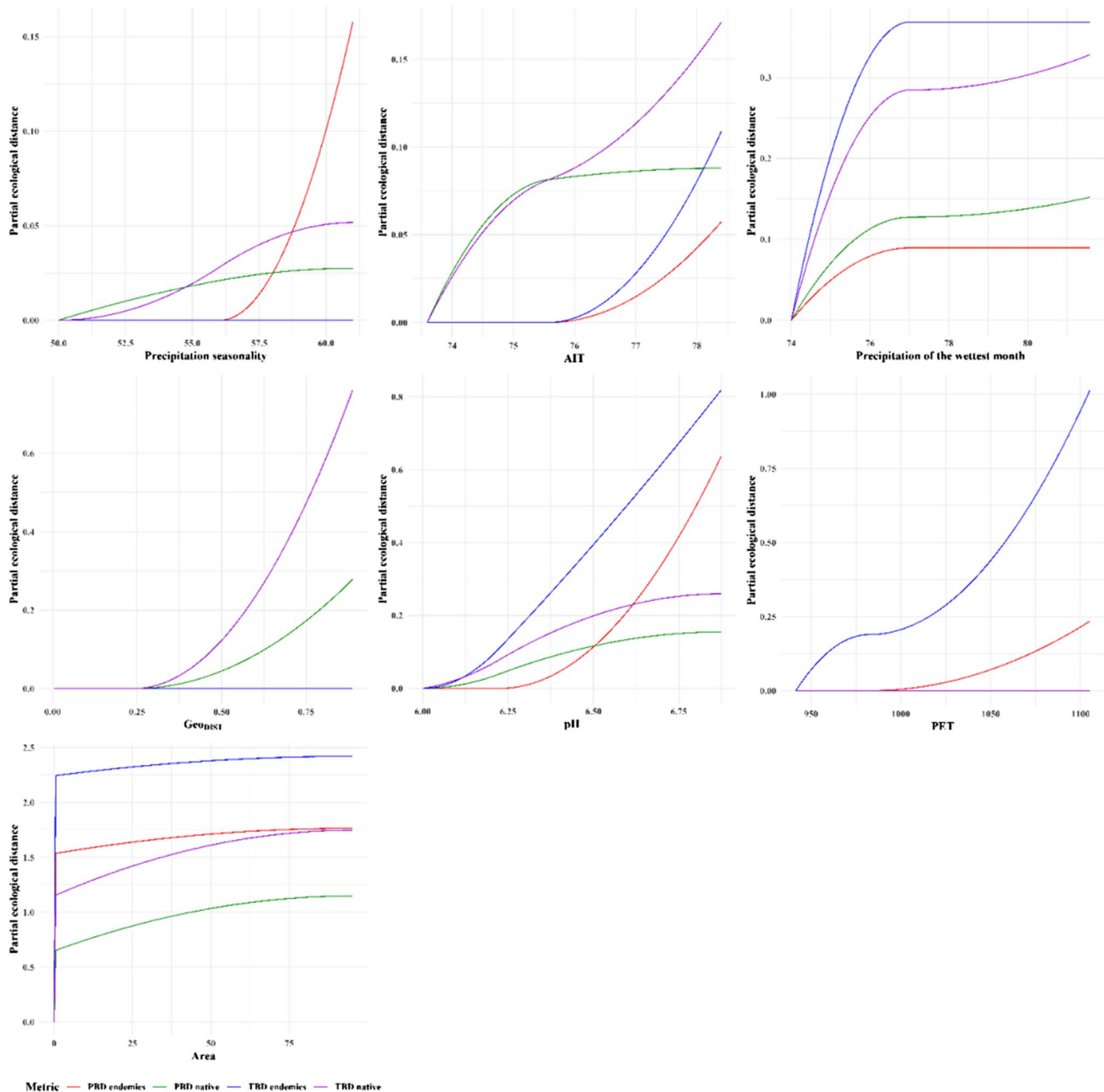


Fig. 4 GDM-fitted I-splines (partial regression fits) for variables significantly associated with endemic (red line) and native (green line) phylogenetic beta diversity, endemic (blue line) and native (purple line) taxonomic beta diversity in the Northern Sporades. The maximum height reached by each curve indicates the total amount of

turnover associated with that variable, holding all other variables constant. The shape of each function indicates the variation of turnover rate along the gradient. *AIT* Thornthwaite aridity index; *PET* annual potential evapotranspiration; *PBD* phylogenetic beta diversity; *TBD* taxonomic beta diversity

in combination with its large size, mountainous landscape and environmental complexity explain why Evvia seems to be biogeographically separated from Northern Sporades, corroborated by the rather low number of WAe endemics occurring on those islands and islets. This is in line with the fact that the endemism rate grew larger the more distant islands and islets were from the adjacent mainland (Table 1);

small islets generally exhibited higher endemism rates than the larger islands.

The only single island endemic of Skiathos is the schizoendemic and obligate chasmophyte *Campanula sciathia* that belongs to the section *Quinqueloculares* (Boiss.) Phitos. The section's taxa and their distributional patterns (*Campanula cymaea* near Kymi, *Campanula constantinii* on Mt

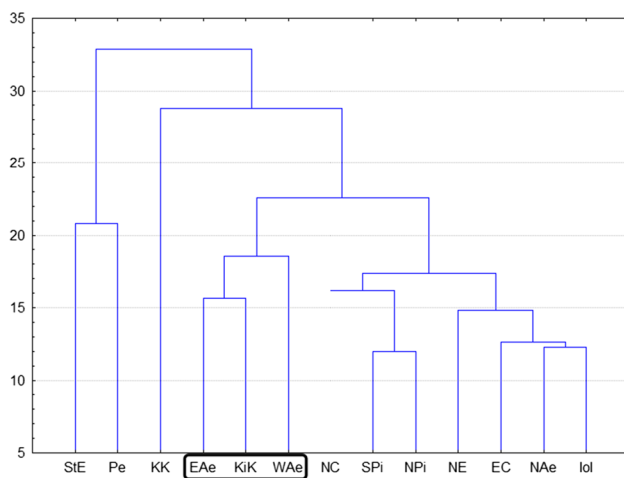


Fig. 5 Hierarchical cluster analysis (linkage method: Ward's method. Euclidean distances) showing floristic relations among floristic regions of Greece, based on the distribution of endemic taxa. *StE* floristic region of Sterea Ellas; *Pe* floristic region of Peloponnese; *KK* floristic region of Kriti-Karpathos; *EAe* floristic region of the East Aegean Islands; *Kik* floristic region of the Kiklades; *WAe* floristic region of the West Aegean Islands; *NC* floristic region of North-Central Greece; *SPi* floristic region of South Pindos; *NPi* floristic region of North Pindos; *NE* floristic region of North-East Greece; *EC* floristic region of East-Central Greece; *NAe* floristic region of the North Aegean Islands; *Iol* floristic region of the Ionian Islands

Dirphis and *Campanula scopelia* found on Skopelos and Kyra Panagia) have emerged as a result of the region's palaeogeographical history (Phitos 1965; Eddie and Ingrouille 1999; Crowl et al. 2015).

Island taxonomic and phylogenetic diversity

Island diversity patterns

Area emerged as the most important variable shaping taxonomic plant diversity (Table 2), while niche-based processes played a lesser role in driving these patterns. This phenomenon is also observed in other Aegean island complexes and biogeographical regions, where niche-based processes play a lesser role in shaping the geographical distribution and species richness patterns of the Aegean island plant communities (Panitsa et al. 2010; Kagiampaki et al. 2011; Kallimanis et al. 2011; Kougiumoutzis and Tiniakou 2014; Kougiumoutzis et al. 2017). On the other hand, island phylogenetic diversity is predominantly determined by climate, implying that the region's spatial configuration plays a minor role in shaping these diversity patterns, a phenomenon also observed in oceanic archipelagos as well (Cabral et al. 2014). This concurs with the presence of niche conservatism in Mediterranean ecosystems (Rundel et al. 2016; Skeels and Cardillo 2017) and with the fact that most endemics

occurring in the Aegean seem to use the same ecological niche (Kallimanis et al. 2011).

Most island and islet floras showed a general tendency for phylogenetic clustering. Nevertheless, Skiathos was the sole exception to this rule, suggesting that the relative importance of different processes shaping species composition varies among the Northern Sporades islands. More specifically, phylogenetic clustering could be due to either increased island isolation, in situ speciation or strong environmental filtering (e.g. Webb et al. 2002; Weigelt et al. 2015). On the other hand, phylogenetic overdispersion could arise from competitive exclusion of closely related species or environmental filtering across multiple habitats on a given island (e.g. Cavender-Bares et al. 2009). The phylogenetic overdispersion observed in Skiathos, the largest island in our study system and the one closer to the adjacent mainland, could be due to reduced environmental filtering, since larger islands tend to be topographically and environmentally more complex and thus provide more opportunities for the establishment and long-term survival of different clades with different niche requirements (Parent and Crespi 2006; Cardillo et al. 2008). Skiathos' flora may have also been enriched with migrating lineages from adjacent mainland regions, due to its longer-lasting connection with Evvia and Sterea Ellas during Pleistocene glacial periods. Putative refugia tend to be phylogenetically over-dispersed (e.g. Kooyman et al. 2011, 2013), a phenomenon recently highlighted for some forest communities in mainland Greece (Mastrogianni et al. 2019).

Beta-diversity patterns and affecting factors

The Mediterranean region's intricate geography and orography (Rundel et al. 2016 and references therein) have resulted in high taxonomic beta diversity (Thompson 2005), a phenomenon apparent in our study area as well, since most Northern Sporades islands and islets have very few endemic species in common (floristic differences range: 15.8–97.1%). The palaeogeographical history of Northern Sporades and the subsequent sea-level and island area changes may have resulted in reduced species dispersal, thus promoting isolation and high beta diversity among the island plant communities, which could be the result of differential allopatric speciation and extinction (e.g. *Campanula sciathia*, *C. scopelia*, *C. rechingeri* and other taxa belonging to the section *Quinqueloculares* (Boiss.) Phitos). Moreover, the responses of endemic PBD were consistently smaller than those of TBD. This implies that phylogenetically close relatives have probably been responsible for the spatial variation in Northern Sporades plant diversity.

Beta-diversity patterns at a global scale are better predicted by topographical heterogeneity as expressed by elevation rather than biotic transitions (e.g. Peixoto et al.

2017), while in the Mediterranean, these patterns seem to be driven by climatic factors as well (e.g. Molina-Venegas et al. 2017; Xystrakis et al. 2019). This concurs with our results, since PBD and TBD patterns are mainly shaped by area and several environmental gradients, such as PET, AIT and PWM (Figs. 2, 3, 4). As in the Ionian archipelago (Valli et al. 2019), geographical distance only plays a minor role in establishing the beta-diversity patterns (Figs. 2, 3, 4), pointing out that dispersal filtering is not the dominant process regarding the assembly of the Northern Sporades island flora. This is in line with previous works stating that climate has also contributed to the biogeographical configuration of the Aegean archipelago (Kougioumoutzis et al. 2014a, 2017; Kougioumoutzis and Tiniakou 2014). This is also in harmony with the fact that nearly 40% of the present Aegean flora (excluding the endemics) has reached the Aegean Islands owing to human action in prehistoric or early historic times (Greuter 1979).

The presence of these human-dispersed species may explain the lesser part dispersal limitation has in shaping the PBD patterns of the Northern Sporades island complex.

Phytogeographical relationships

Our results on phytogeographical relations are based on the analysis of the Greek endemic taxa for two reasons: (1) when we ran the analysis based on the total number of taxa (i.e. the native taxa), the results were similar, yet the trends not so obvious as those obtained from the Greek endemics and more importantly, (2) when dealing with phytogeographical issues in the Aegean, only these taxa, rather than the whole flora, are phytogeographically meaningful and informative (Greuter 1975).

Most of the island and islet pairs showed rather high floristic dissimilarity, with the notable exception of Yioura and Kyra Panagia. The flora of these islands is very similar and is probably the result of their long-lasting isolation from the other Northern Sporades islands and islets (Kamari et al. 1988; Snogerup 1991; Snogerup et al. 1991). The vast majority of taxa occurring on Yioura and Kyra Panagia are relicts of different age which may have survived on these two islands due to the long-lasting isolation that may have hindered the arrival and establishment of competitors (Snogerup 1991). The high floristic similarity between Yioura and Kyra Panagia is in harmony with the land connection between these two islands since the late Messinian, c. 4.5 Mya (Kamari et al. 1988—Online Resource 3).

Hierarchical cluster analyses based on the taxonomic and phylogenetic diversity of Greek endemics (Online Resource 3) divided the Northern Sporades into distinct groups clearly based on area and elevation of the islets and islands, as these factors according to Kallimanis et al. (2011) and

Kougioumoutzis et al. (2017), are the major drivers of plant diversity patterns in the Aegean area.

West Aegean islands (WAe) were grouped with Kiklades (Kik) and East Aegean islands (EAe) based on the distribution of Greek endemic taxa. On the other hand, Evvia which is phytogeographically very well separated from the Northern Sporades clusters together with Sterea Ellas and Peloponnisos.

According to Georghiou and Delipetrou (2010), the Northern Sporades show higher phytogeographical affinities to the adjacent mainland regions of Sterea Ellas, East-Central Greece and the Peloponnese (StE, EC and Pe, respectively) and then with the phytogeographical region of the Kiklades (Kik). According to our results, seven taxa are biregional endemics [i.e. taxa useful for inferring phytogeographical relationships in the Aegean (Kougioumoutzis et al. 2012a, 2012b, 2014b, 2015)] and three of them—namely *Campanula reiseri*, *Erysimum senoneri* subsp. *senoneri* and *Fritillaria ehrhartii*—are exclusively found in WAe and Kik, two occur exclusively in WAe and EAe (*Centaurea rechingeri* and *Linum gyaricum* subsp. *gyaricum*), while only one occurs either in NAe or EC.

Therefore, we argue that the Northern Sporades seem to be closer connected to Kik and EAe rather than to StE, EC and Pe as previously suggested for the entire WAe phytogeographical region (Georghiou and Delipetrou 2010), which was probably heavily influenced by the inclusion of Evvia—an entity entirely different from the Northern Sporades island complex in biogeographical terms (Kougioumoutzis et al. 2017).

Our results thus lend weight to the hypothesis that the Northern Sporades (along with Skyros) seem to be closer connected to the Kiklades rather than to Evvia or the adjacent mainland, due to their longer isolation and separate palaeogeographical history during the Quaternary (Sakellariou and Galanidou 2017; Simaiakis et al. 2017). These results are also in accordance with the findings of Kougioumoutzis et al. (2017) that two main distributional and (palaeo-) geographical barriers exist in the Aegean Archipelago: the Mid-Aegean trench and the North Aegean Trough that limit the phytogeographical connections between the Northern Sporades with Kriti and North Aegean islands, respectively.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Information on Electronic Supplementary Material

Online Resource 1. Abbreviations and correlation matrix of all the abiotic variables included in the analyses. Standardized effect scores of the phylogenetic alpha diversity for each island and islet included in the analyses. Dissimilarity matrix based on Sørensen's index.

Online Resource 2. List of species occurring in the Northern Sporades islands and islets complex.

Online Resource 3. **a** Numbers of vascular plant taxa in the flora of the Northern Sporades islet complex. **b** Life forms in the total (1202 taxa) and the endemic (41 taxa) native flora of the Northern Sporades islet complex. **c** Chorological spectrum of the native flora of the Northern Sporades island complex. **d** Families with Greek-, WAe- and Single-Island endemics and degree of endemism. **e** Hierarchical cluster analysis showing floristic relations between the Northern Sporades islet complex based on the phylogenetic diversity (PBD) of Greek endemic taxa. **f** Hierarchical cluster analysis showing floristic relations between the Northern Sporades islet complex based on the taxonomic diversity (TBD) of Greek endemic taxa.

Online Resource 4. The phylogenetic tree of the species included in our analyses based on the GBMB phylogenetic tree published by Smith & Brown (2018).

Online Resource 5. Plant species of special biogeographical interest.

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