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Determinants of alpha and beta vascular plant diversity in Mediterranean island systems: the Ionian islands, Greece

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The Ionian archipelago is the second largest Greek archipelago after the Aegean, but the factors driving plant species diversity in the Ionian islands are still barely known. We used stepwise multiple regressions to investigate the factors affecting plant species diversity in 17 Ionian islands. Generalized dissimilarity modelling was applied to examine variation in the magnitude and rate of species turnover along environmental gradients, as well as to assess the relative importance of geographical and climatic factors in explaining species turnover. The values of the residuals from the ISAR $\log_{10}$-transfomed models of native and endemic taxa were used as a measure of island floristic diversity. Area was confirmed to be the most powerful single explanatory predictor of all diversity metrics. Mean annual precipitation and temperature, as well as shortest distance to the nearest island are also significant predictors of vascular plant diversity. The island of Kalamos constitutes an important plant diversity hotspot in the Ionian archipelago. The recent formation of the islands, the close proximity to the mainland source and the relatively low dispersal filtering of the Ionian archipelago has resulted in islands with a flora principally comprising common species and a low proportion of endemics. Small islands keep a key role in conservation of plant priority sites.

Keywords: species richness, endemism, island biogeography

Introduction

Islands contribute disproportionately to global biodiversity, since they comprise just 3.5% of earth's land area but host 15–20% of all terrestrial species (Whittaker et al. 2017). Thus, islands are of key interest for studies and experimental research in ecology, biogeography and evolution (Denslow 2001). They have additional research advantages compared to mainland areas, as they are comparatively small, have distinct boundaries, their biotas are usually less complex than those of the adjacent mainland, and ecological and evolutionary processes are relatively easier to detect on islands due to their geographical isolation (Whittaker and Fernández-Palacios 2007). Islands also play a major role in the contemporary extinction crisis, as more than

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60% of the documented terrestrial species extinctions since 1500 CE have been island endemics (Johnson et al. 2017, Whittaker et al. 2017). Consequently, islands are particularly important for the conservation of global biodiversity (Caujapé-Castells et al. 2010).

The Mediterranean basin is one of the 35 major global terrestrial biodiversity hotspots (Médail and Myers 2004). The Mediterranean islands, which are mainly of continental origin, contain numerous endemic and range-restricted plants (Thompson et al. 2005, Vogiatzakis et al. 2008, Médail 2013). Their high plant diversity reflects their palaeogeographical history (Médail and Quézel 1999). Most Mediterranean islands belong to the two Greek archipelagos, with ca 7600 islands and islets in the Aegean archipelago and ca 300 islands and islets in the Ionian (Médail 2017).

The Ionian archipelago is located at the eastern half of the Mediterranean basin, in western Greece (Fig. 1). The size and elevation of individual islands range from 0.015 to 734 km^2 and from 12 to 1628 m a.s.l., respectively. They form a distinct phytogeographical region, (IoI – sensu Dimopoulos et al. 2013) that hosts 2027 plant taxa, 1827 of which are native and 89 are Greek endemics (Dimopoulos et al. 2013, 2016, Flora Ionica Working Group 2016–). In the Ionian archipelago, 21 sites have been included in the Natura 2000 network of protected areas, underlying the need to protect and preserve the biodiversity in this region. The ecological importance of the Ionian islands is also highlighted by the existence of two National Parks (the Ainos National Park and the Zakynthos National Marine Park), while Echinades islets (islands no. 1–4 in Fig. 1) are part of a National Park that also includes mainland areas. The Ionian islands belong to the Mediterranean climatic belt, while along this area some of the highest central Mediterranean precipitation heights have been recorded (Kolios and Kalimeris 2017).

The origin and distribution patterns of the Greek flora have previously been related to palaeogeographical patterns (Turrill 1929, Rechinger 1965). The Ionian islands play a major role in the geodynamic framework of the central Mediterranean, constituting a multiple junction region (Accordi et al. 2014), where three tectonic plates meet (African plate, Eurasian plate and Adriatic micro-plate). The palaeogeographical history of the Ionian islands is rather recent, as most islands became separated from the adjacent mainland during the Pleistocene or even later (Perissoratis and Conispoliatis 2003, Triantis and Mylonas 2009).

During Pleistocene's glacial and interglacial periods, sea-level fluctuations have repeatedly increased island area, bringing islands closer to each other and to the adjacent mainland (Shackleton 1987), thus reducing island isolation and favoring species' colonization (Blondel et al. 2010). More specifically, 21.5 thousand years ago (Kya) the sea-level was ca 120 m lower than today (Perissoratis and Conispoliatis 2003), resulting in the fusion of the Ionian islands with western Greek mainland. A narrow strait separated the landmass of Kefalonia, Ithaki and Zakynthos from Lefkada; the latter

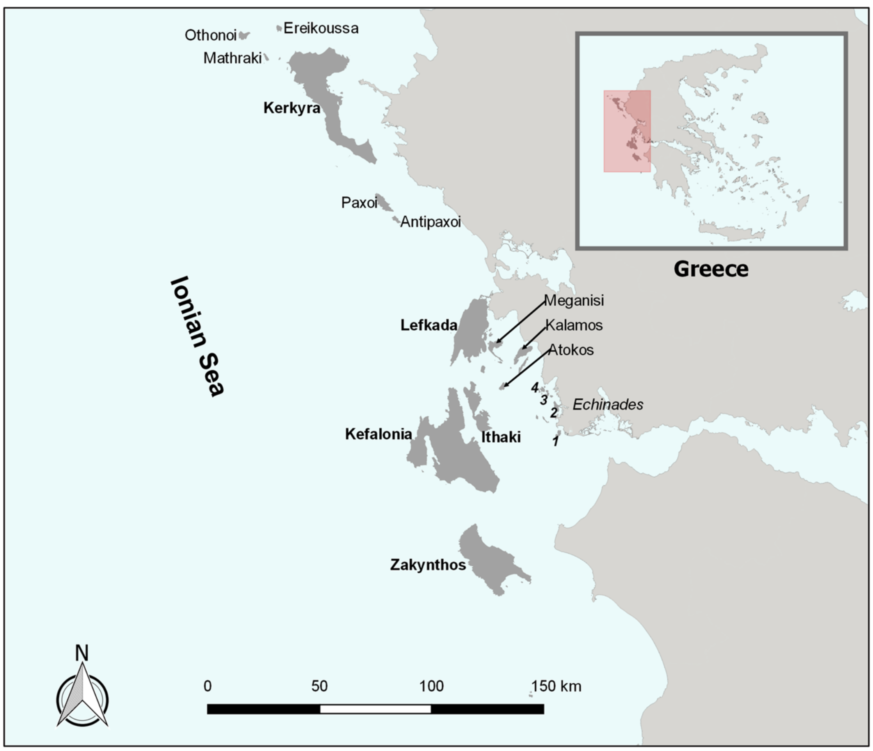

Figure 1. The Ionian islands included in the present study. Numbers correspond to the islets that belong to Echinades islets group as follows: 1 = Oxeia, 2 = Petalas, 3 = Provati, 4 = Dragonera.

formed a mainland peninsula, and was connected with most of its small, satellite islets (i.e. Meganisi, Skorpios, Kastos and Kalamos). Arkoudi and Atokos were the only islets that remained isolated during this period (Ferentinos et al. 2012, Zavitsanou et al. 2015). At the same period, Kerkyra was connected with the adjacent mainland. Subsequently, 18 Kya the sea-level started rising rapidly (Fairbanks 1989, Perissoratis and Conispoliatis 2003). The present day configuration of the Ionian islands arose during the Holocene (ca 9–8 Kya), when they became permanently separated from the mainland and were detached from each other.

The Aegean archipelago has attracted the attention of many biogeographers and factors affecting plant species richness in the Aegean Sea are well studied (Strid 1996, Panitsa et al. 2006, Kallimanis et al. 2010, Kagiampaki et al. 2011, Kougioumoutzis and Tiniakou 2014, Kougioumoutzis et al. 2014, 2017). In contrast, there are only few similar studies in the Ionian archipelago. Only two macroecological studies have been carried out (Panitsa and Iliadou 2013, Iliadou et al. 2014a). Moreover, the majority of the biogeographical studies on the Greek islands have focused on island diversity patterns (Triantis et al. 2008, Panitsa et al. 2010, Kallimanis et al. 2010, Trigas et al. 2012, Sfenthourakis and Triantis 2017), while there are just a few studies investigating factors affecting beta-diversity (Fattorini 2006, Panitsa et al. 2008, Sfenthourakis and Panitsa 2012).

Beta-diversity compared to species richness (alpha-diversity), allows testing of different hypotheses about the processes driving species distributions and biodiversity. Beta-diversity can be partitioned into species turnover and nestedness (Baselga and Orme 2012) and this is essential for the investigation of the relative importance of environmental and spatial drivers. Unraveling the drivers of beta-diversity patterns in the Ionian archipelago would increase our knowledge on the factors shaping species assemblages on continental island systems.

The aim of the present study is to investigate the effect of biotic and abiotic factors shaping plant species diversity in a rather overlooked Greek archipelago, since our knowledge of the ecological and evolutionary factors driving plant species assemblages in the Ionian Islands remain vague and narrative. To our knowledge, regression modeling techniques have not before been applied to disentangle the role of several biogeographical factors in shaping native plant assemblages in the Ionian archipelago. Additionally, for the first time, we aim to analyze the beta-diversity in the Ionian islands, as well as to assess the role of individual islands as reservoirs of plant diversity. Particularly, we have addressed the following questions: 1) how does richness vary as a function of area and which are the key factors that affect native and endemic plant species richness in the Ionian islands? 2) which are the most important drivers of beta-diversity in the Ionian archipelago? and 3) are there any islands that can be regarded as plant diversity hotspots in the Ionian archipelago?

Material and methods

Data

We compiled a presence/absence island-plant matrix for the Ionian archipelago, containing 17 islands and 1827 native plant taxa (species and subspecies, N). We excluded from the analyses all islands with a surface area < 1 km^2 or with incomplete floristic data (i.e. Kastos). All alien and naturalized taxa were also excluded from the analyses. Species nomenclature followed Dimopoulos et al. (2013).

We used plant distributional data available from the Flora Ionica Working Group (2016– and references therein), as well as some additional unpublished plant records reported by the first author, in order to compile our matrix. Endemicity of plants was estimated at different levels (Panitsa et al. 2010), as follows: the total number of endemics (TE) of a single island was the sum of the taxa that have a distribution range restricted to Greece (i.e. Greek endemics) and Ionian endemics (IoE) were taxa with their distribution range limited to the Ionian archipelago (Strid and Tan 1997). Ionian endemics (IoE) were used only for the identification of Ionian plant diversity hotspots (hotspot analysis), as their number represents only 1.3% of the overall species richness. Furthermore, we did not include single island endemics in our analyses, since the vast majority of the Ionian islands do not host such taxa (with the exception of Zakynthos, Kefalonia and Lefkada). The numbers of N, TE, (which constitute the response variables) and IoE, as well as the geographical, climatic, geological and topological data of the Ionian Islands are shown in Table 1.

Best subset regression analysis of alpha- and beta-diversity

In order to explore the effect of key biological, geographical and climatic variables on species richness of the Ionian islands, the determinants of the two species richness metrics (N and TE) were modeled by two complementary approaches: 1) the island species-area relationships (ISARs) and 2) best subset regression analysis (Burnham and Anderson 2002). We also applied best subset regression analysis on beta-diversity and its components for N.

ISARs were investigated for the Ionian islands by fitting the logarithmic transformation of the Arrhenius (1921) power model (power function model hereafter), $\mathrm{Log}(S) = c + z \times \mathrm{Log}(A)$, where S is the value of each of the richness metrics used (N and TE), A is the area of the respective island in km^2 and c, z the fitted parameters. A value of 1 was added to all the dependent variables except N 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

Table 1. Plant species richness and values of the explanatory variables used for the Ionian islands included in the present study. N, TE and IoE are the number of total native, Greek endemic and Ionian endemic taxa respectively. A = area (km^2); E = maximum elevation (m); D_m = shortest distance from the nearest mainland (km); D_i = shortest distance to the nearest island (km); G = number of geological substrates; HD = human population density (people km^{-2}); T = mean annual temperature (°C × 10); P = mean annual precipitation (mm).

Island	A	E	D_m	D_i	G	HD	T	P	N	TE	IoE
Antipaxoi	4.1	103	21.7	15.5	1	0.0	170.8	1044.8	227	6	3
Atokos	4.4	181	17.6	8.9	3	0.0	174.4	956.0	234	8	1
Dragonera	2.4	128	1.5	10.7	1	0.0	175.3	922.7	144	0	0
Ereikoussa	3.7	137	27	11	1	134.3	166.0	1109.6	348	2	1
Ithaki	96.0	806	29.3	2.9	7	0.0	166.4	989.4	874	28	8
Kalamos	25.0	745	2.5	13.1	5	19.9	163.4	980.8	610	23	5
Kefalonia	734.0	1628	32.6	2.9	14	45.3	160.4	1005.2	1311	65	14
Kerkyra	592.0	914	2.2	2.2	12	165.5	161.5	1167.5	1484	32	6
Lefkada	325.0	1158	0.1	8.4	7	68.1	155.8	1030.8	1180	58	11
Mathraki	3.1	152	37.7	8	1	60.0	168.5	1067.5	239	1	1
Meganisi	22.4	301	8.9	15	3	46.5	172.5	975.0	428	11	3
Othonoi	10.8	393	41.3	21	2	66.3	162.3	1042.7	315	4	2
Oxeia	4.3	421	1.2	28.6	1	0.0	175.5	885.0	253	3	1
Paxoi	25.3	231	15.6	13.4	2	73.7	167.6	1067.7	549	7	3
Petalas	5.5	250	1.3	19.2	1	0.0	175.3	901.7	161	1	0
Provati	1.2	75	2.5	26.9	1	0.0	178.0	907.0	141	0	0
Zakynthos	406.0	756	18.4	14.9	10	100.2	172.1	964.0	1122	36	11

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). The z parameter was used for preliminary comparison between the floristic diversity of the Ionian islands.

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.

The explanatory variables were island area (A, km^2), maximum elevation (E, m), shortest distance to nearest mainland and island (D_m and D_i, respectively, km), number of geological substrates (G), human population density (HD, people km^{-2}), as well as mean annual temperature and precipitation [T and P (°C × 10, mm), respectively]. The variables A, E, D_i, and D_m were determined from 1:50 000 scale digital topographic maps obtained from the Hellenic Military Geographical Service (web.gys.gr/GeoSearch/). The number of geological substrates (G) was compiled from the 1:500 000 scale geological map of Greece (Bornovas and Rondogianni-Tsiambaou 1983). From these, 18 different types of geological substrates were considered, while the most dominant substrates are limestones and Triassic breccias (remnants of weathered gypsum). We used WorldClim 30-arc second climate products (Hijmans et al. 2005) to calculate the climatic variables; T and P were obtained from the CCSM4 model and were statistically downscaled to a 2.5-arc minute resolution (Hijmans et al. 2005). Data regarding HD was extracted from the Hellenic Statistical Authority's report (2011). By fitting the full model, the total adjusted coefficient of multiple determination (R^2_{adj}) was assessed. Spearman's correlation coefficient was used for all pairwise correlations among species richness metrics. Two explanatory variables (E and G) were excluded from the analyses because they were highly collinear with area (Supplementary material Appendix 1 Table A1). In order to examine the relative importance of each predictor variable in driving species turnover, we also used the geographical distance between the Ionian islands (G_D).

Finally, in order to compare the floristic diversity between islands of different size and locate possible Ionian plant diversity hotspots, we used the values of the residuals from the ISAR log_{10}-transfomed models of species richness metrics (N and TE) as well as IoE, as these values are interpreted as a measure of island species diversity and do not reflect the influence of island area (Hobohm's α-index, Hobohm 2000, 2003). Positive and negative values of this Hobohm's α-index refer to areas with species diversity above and below average, respectively (Hobohm 2000, 2003).

All analyses and graphs were carried out in the R 3.3.2 (R Development Core Team) using core functions and functions from the 'leaps' (Lumley 2009) and 'ggplot2' (Wickham 2009) packages.

Generalized dissimilarity modelling

We used Generalized dissimilarity modelling (GDM – Ferrier et al. 2007) to model pairwise plant community compositional dissimilarity (quantified with the Sørensen measure) between all the Ionian islands included in our analysis as a response to environmental and spatial variables. 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). All GDM analyses were performed with the 'gdm' 1.3.7 (Manion et al. 2018) package.

Results

Species richness

The total number of taxa (N) occurring in the island-plant matrix for the Ionian archipelago was 1827. Eighty-nine taxa (5%) are Greek endemics, while 23 of them (1.3%) are endemics to the Ionian islands. The number of native taxa per island varied from 141 to 1473 (Table 1). The proportion of Greek and Ionian endemics in individual island floras ranged from 0.0 to 5.0% and 0.0 to 1.1%, respectively.

Species-area relationships

The ISAR power function model explained a higher proportion of variance for N than TE (Supplementary material Appendix 1 Table A2). Nevertheless, TE increased with increasing area more steeply than N.

Predictors of species richness

Simple linear regressions of species richness metrics were applied in order to compare the performance of the explanatory variables (Supplementary material Appendix 1 Table A1). The analyses confirmed A as the most powerful single explanatory variable of island plant species richness, while E, T and G also explained a large proportion of the variance for almost all species richness metrics (Supplementary material Appendix 1 Table A2).

Predictive modelling

Alpha-diversity

Area (A) and P were retained in the optimal model for N, while A together with T, D_m, D_i and HD were retained in the optimal model for TE (Table 2).

Generalized Dissimilarity Modelling

Our GDM models explained 66.9% and 46.2% of the deviance for the native and endemic taxa, respectively. The most important gradient for both native and endemic taxa was area, followed by mean annual temperature and geographical distance, respectively (Fig. 2–3). The fitted functions describing the turnover rate and magnitude along each gradient were not linear; the turnover rate varied with position along gradients and was greatest at low levels of spatial extent for both metrics and at the high end of the temperature gradient (Fig. 3). More specifically, the Ionian

Table 2. Summary statistics for predictive models of N and TE, regarding alpha-diversity with A, D_m, D_i, HD, T and P as proposed by the best subset regression. All variables were log_{10}-transformed. The adjusted R^2 (total variance explained by each model), 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. Abbreviations as in Table 1.

	Est.	t	p	p_{Bon}	AIC	R^2_{adj}	r_w	F	p-value
N					–31.90	0.94	–	136	< 0.001
Intercept	–2.81	–1.42		–	–		–		
A	0.34	14.28	0.00	0.00	–		86.2		
P	1.66	2.50	0.03	0.05	–		14.8		
TE					6.41	0.84	–	17.4	< 0.001
Intercept	24.32	1.78			–		–		
A	0.64	5.89	0.00	0.00	–		56.8		
T	–10.99	–1.78	0.10	0.50	–		21.1		
D_i	0.32	1.16	0.27	1.00	–		14.0		
HD	–0.17	–1.76	0.11	0.55	–		7.7		
D_m	0.12	1.29	0.22	1.00	–		0.4		

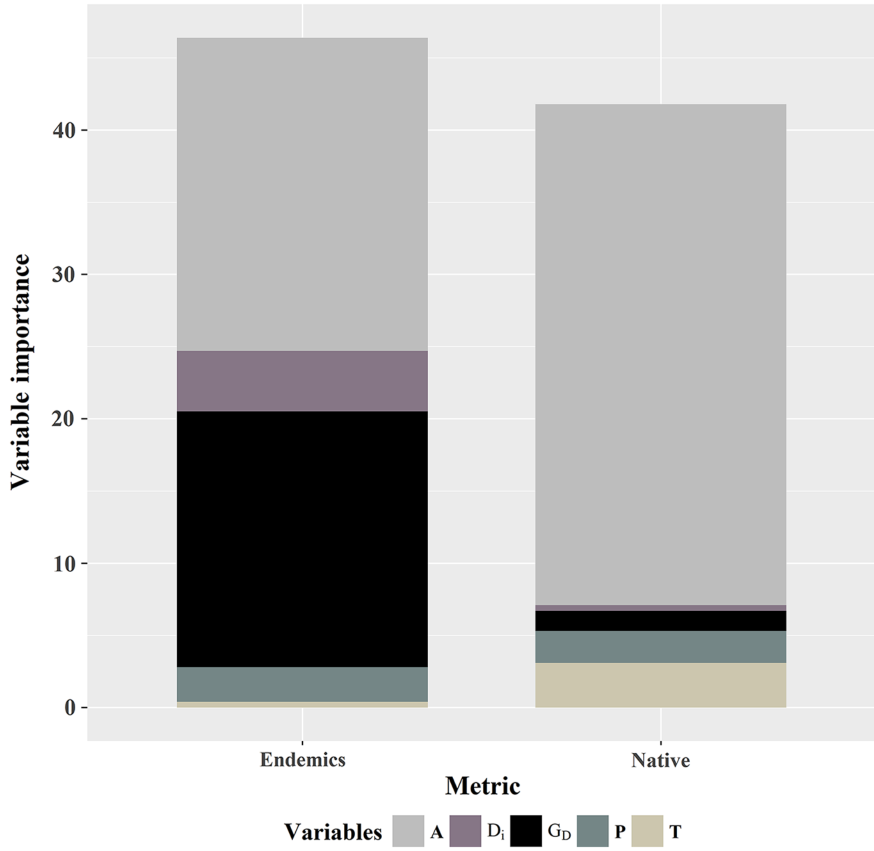

Figure 2. The relative importance of each predictor variable in driving beta-diversity. Abbreviations as in Table 1. G_D = Geographical distance between the Ionian islands.

plant communities (native or endemic) differed significantly even at areas ca 30 km^2 and their composition continued to change with a rapid, but less abrupt trend until the 400 km^2 threshold (Fig. 3). Isolation metrics (geographical distance or distance from mainland) had a more profound effect on the endemic plant communities (Fig. 3). Furthermore, climate played an important role in shaping native and endemic plant assemblages in the Ionian archipelago. The endemic plant communities changed rapidly until a plateau was reached at ca 1000 mm of mean annual precipitation (Fig. 3). Finally, a turning point was observed at ~17°C for the native plant assemblages, where they started to differ more swiftly (Fig. 3).

Locating plant diversity hot-spots

Using the α-index (Table 3), Ereikoussa and Kalamos presented values well above average regarding native taxa richness (2.06 and 1.37 respectively), whereas Petalas displayed the lowest value (–2.29). Two islands could be regarded as floristically impoverished (very low α-values): Dragonera and Petalas. For TE, Atokos and Kalamos have remarkably high values (1.81 and 1.69 respectively), while Dragonera has the lowest value (–1.67). Ereikoussa is a diversity hotspot among the Ionian islands, Antipaxoi and Atokos are endemism hotspots, while Kalamos is both a diversity and an endemism hotspot (Fig. 4).

Discussion

Patterns of alpha-diversity

Species–area relationships

The increase in species richness with area is one of the few law-like regularities in ecology (Rosenzweig 1995, Storch 2016, Whittaker et al. 2017). Area is the most powerful single explanatory variable of species richness in both oceanic and continental island systems (Panitsa et al. 2006, Whittaker and Fernández-Palacios 2007, Triantis et al. 2008, 2012, Kagiampaki et al. 2011, Kougioumoutzis and Tiniakou 2014). In the present study, species richness and area are strongly related for the diversity metrics used, namely the native taxa (N) and the total number of endemics (TE). Our power function model has an overall predictive capacity of $R^2 = 0.93$ and is consistent with the R^2-value reported for the ISAR power function model of 488 islands across the globe (Kreft et al. 2008). It is also in line with the R^2 value reported for the Echinades islets group ($R^2 = 0.84$, Iliadou et al. 2014b) and for some Ionian islands ($R^2 = 0.89$, Iliadou et al. 2014a).

The z-value is an important parameter that reflects the increase of species richness with increasing surface area. High z-values are associated with high isolation, and consequently

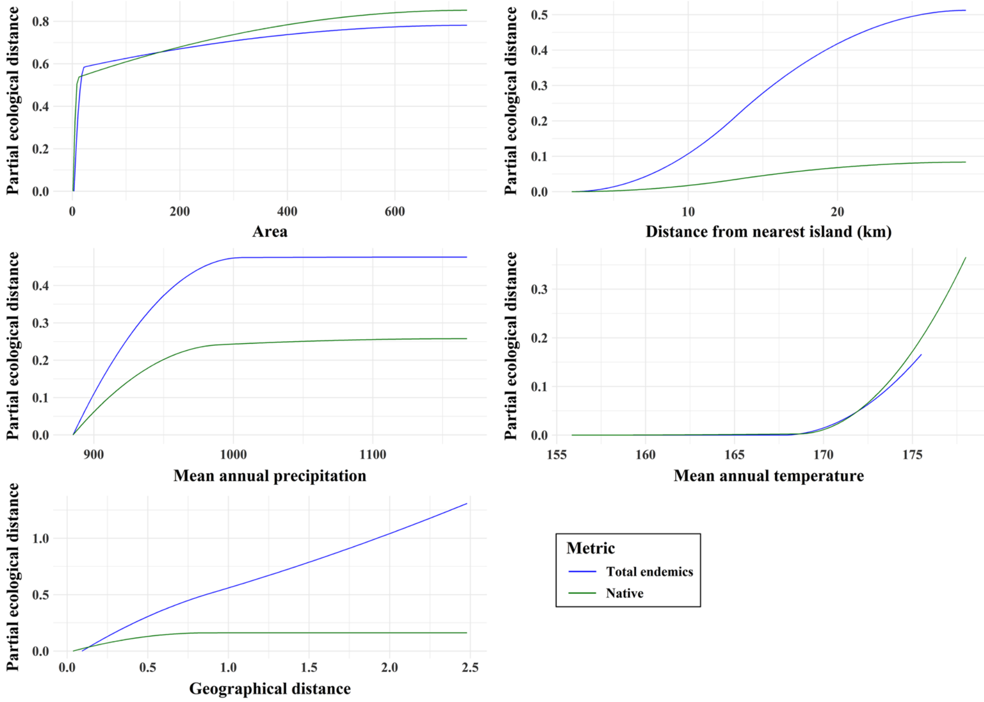

Figure 3. GDM-fitted I-splines (partial regression fits) for variables significantly associated with native (green line) and endemic (blue line) plant beta-diversity in the Ionian archipelago. The maximum height reached by each curve indicates the total amount of turnover associated with that variable, holding all other variables constant. The shape of each function indicates the variation of turnover rate along the gradient.

low immigration rates (Triantis et al. 2012, Matthews et al. 2016). In our study, the ISAR z value (z = 0.37) fell within the range of 0.2–0.45 proposed by Whittaker and Fernández-Palacios (2007) for insular systems, as in the case of other Greek island complexes. In particular, the z-value for the east Aegean islands is 0.326 (Panitsa et al. 2010), for the south Aegean islands is 0.39 (Kagiampaki et al. 2011) and for the Cyclades is 0.43 (Kougioumoutzis and Tiniakou 2014). The z-values of off-shore island groups (i.e. Ionian and east Aegean islands) are smaller compared to that of more isolated island complexes (i.e. Cyclades, South Aegean islands), which can be attributed to their palaeogeographical history (Wang et al. 2010, Hu et al. 2011, Ding et al. 2013). Consequently, shallow slopes characterize island groups with minimal isolation, such as the Ionian islands, in which a rescue effect could be observed and therefore explains the higher species richness on smaller islands (Whittaker et al. 2017). Finally, according to our results, TE has the highest z-value. The recent formation and low isolation of the Ionian islands probably promote the colonization of TE in our study system.

Table 3. Values of the α-index for the total native (N), the Greek endemic taxa (TE) and the Ionian endemic taxa (E). Abbreviations as in Table 1.

Island	Alpha-N	Alpha-TE	Alpha-IoE
Antipaxoi	–0.16	1.42	2.02
Atokos	–0.14	1.81	0.01
Dragonera	–1.44	–1.67	–1.31
Ereikoussa	2.06	–0.05	0.20
Ithaki	0.76	0.57	0.88
Kalamos	1.37	1.69	1.18
Kefalonia	–0.93	–0.16	0.12
Kerkyra	0.12	–1.24	–1.92
Lefkada	0.07	0.57	0.38
Mathraki	0.58	–0.62	0.39
Meganisi	–0.10	0.53	0.19
Othonoi	–0.29	–0.28	0.17
Oxeia	0.29	0.33	0.04
Paxoi	0.86	–0.35	0.05
Petalas	–2.29	–1.24	–2.15
Provati	–0.31	–0.90	–0.55
Zakynthos	–0.59	–0.61	0.13

Factors affecting plant species richness

Area and precipitation emerged as the variables most positively influencing plant species richness in the Ionian islands (Table 2). The importance of water availability (and precipitation as its proxy) in ecosystems ranks precipitation among the most significant climatic variables (Kalimeris et al. 2012). It has already been documented in several studies (Kreft and Jetz 2007, Sommer et al. 2010, Kougioumoutzis and Tiniakou 2014) that water availability imposes a limiting factor regarding plant species richness. High species richness likely results from high resource availability and low selective pressure for specialization, suitable for common species (Stohlgren et al. 2005, Weigelt et al. 2013). The Ionian islands are characterized by a humid climate (Krigas et al. 2010) and

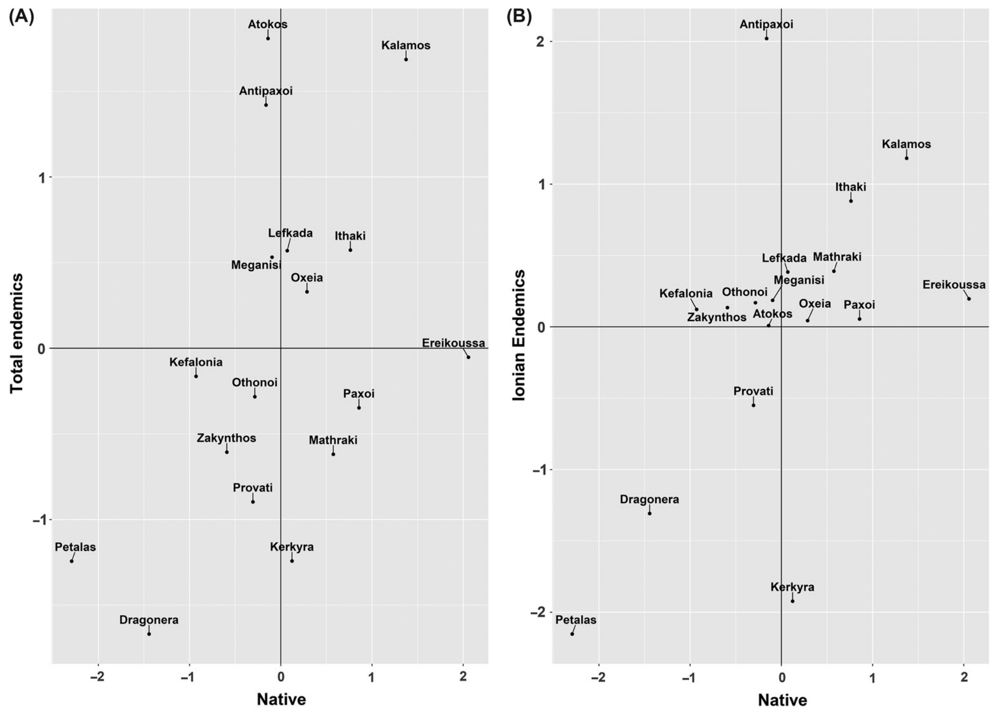

Figure 4. (A) Plot of residuals of total endemics (y-axis) versus native taxa (x-axis) and (B) plot of residuals of the Ionian endemics (y-axis) versus native taxa (x-axis), as estimated from the ISAR power function model for Dataset-1.

dense vegetation, which is primarily dominated by common species (Iliadou et al. 2014a), features shared with the continental species pool of western mainland Greece (Kolios and Kalimeris 2017). As islands receive colonizers from climatically similar areas (Weigelt and Kreft 2013), colonization of the Ionian islands is expected to have been unhindered, increasing their plant species richness.

Factors affecting endemic plant species richness

Our results support a strong negative effect of mean annual temperature on TE (Table 2). Furthermore, there is a strong negative correlation between mean annual precipitation and mean annual temperature in the Ionian islands. According to Sommer et al. (2010), in humid regions, such as Ionian islands, with positive water balance, there is a clear positive relationship between the regional capacity for plant species richness and temperature. In a global model for contemporary plant species richness, the relationship between temperature and water availability appeared to be a major limiting factor of the species number a certain region can maintain (Kreft and Jetz 2007, Sommer et al. 2010). In areas with humid conditions, a positive relationship between species richness and temperature was found, i.e. the warmer the temperature, the higher the corresponding species richness (Zachos and Habel 2011). However, the degree of endemism often decreases as floristic richness increases, possibly due to interspecific competition (Médail and Verlaque 1997). The Ionian islands are characterized by a dense vegetation cover, limiting endemic plant taxa to particular habitats with low disturbance and high stress level (Trigas et al. 2008, Georgiou and Delipetrou 2010 and references therein), such as rocky habitats, calcareous cliffs and slopes. Thus, it seems that temperature has an indirect strong negative effect on endemic plant species richness.

Another possible explanation of the strong negative effect of temperature on the endemic plant species richness comes from its relation to elevation (excluded from the analyses as collinear with A – Supplementary material Appendix 1 Table A1). Decreasing temperature with increasing elevation is widely accepted as a general pattern (Barry 2008). Moreover, endemic species richness usually peaks at higher elevations (Trigas et al. 2013). Topographic complexity may cause gene-flow barriers among diverging populations, supporting reproductive isolation and hence local differentiation (Gillespie and Roderick 2014). Topography-driven isolation increases speciation rates in mountainous areas, resulting in a globally consistent pattern of higher endemism at higher elevations (Steinbauer et al. 2016). The large and mountainous islands of Kefalonia and Lefkada, together with Zakynthos, are the richest islands in terms of Ionian endemics. They are also the only islands that host single island endemics in the Ionian archipelago. As topographic isolation has been related to increased endemism, the low elevation of most Ionian islands seems to be an additional cause of low endemism in the Ionian archipelago (the other being the recent isolation).

Geographical distances (D_i and D_m) have a positive effect on TE. During the Pleistocene glacial and interglacial periods, connections among many Ionian islands and adjacent mainland were established or broken in a chained sequence of events (Shackleton 1982), while the final formation of the Ionian islands took place during the Holocene (ca 9–8 Kya). The positive effect of geographical distances on endemism indicates that the established inter-island and island-mainland land-bridges during Pleistocene low sea level stages have filtered the distribution of at least some plant lineages.

Human population density (HD) appeared to have a negative effect on TE. Global human activity is affecting species richness, in particular through land-use changes and pollution (Pautasso 2007). The negative effect on TE possibly reflects the effect of the continuous human presence over several millennia in the Ionian islands (Triantis and Mylonas 2009), which are less resistant and resilient to disturbance than mainland areas, a phenomenon also apparent in the central Aegean archipelago (Kougioumoutzis and Tiniakou 2014). Habitat loss as a result of human activities (e.g. tourism, agriculture, animal husbandry) constitutes a major threat for the endemic plants (Trigas et al. 2012).

Beta-diversity patterns

Mediterranean plant communities are characterized by high species turnover along sharp environmental gradients (Molina-Venegas et al. 2016 and references therein). Globally, beta-diversity patterns are best predicted by elevation rather than biotic transitions (Peixoto et al. 2017 and references therein), while extreme temperature (and precipitation) variation occurring over short geographical distances gives rise to increasing beta-diversity (McKnight et al. 2007, Melo et al. 2009, König et al. 2017). This aligns with our results, since in the Ionian archipelago, beta-diversity patterns are primarily driven by area – which is highly collinear with elevation – and temperature (Fig. 2–3). Local island environmental conditions create rather strong filters, thus reducing the set of potential colonizers from the adjacent mainland and hence result in the biotic homogenization of island plant communities (König et al. 2017). The aforementioned patterns are less affected by geographical distance (inter-island or island-mainland distance), suggesting that dispersal filtering plays a minor role in shaping native island plant assemblages in the Ionian. The recent isolation of the Ionian islands and the short distances that separate them from mainland Greece also support this aspect. Nevertheless, dispersal limitation, as expressed by the isolation metrics (D_i and D_m), seems to play an important role in driving endemic beta-diversity patterns in the Ionian archipelago (Fig. 2–3).

Plant diversity hotspots

A promising approach for the long-term maintenance of biodiversity is to identify biodiversity hotspots (sensu Myers et al. 2000). The most frequently applied criterion by conservationists is endemicity (Cañadas et al. 2014). In Greece, most endemic plant taxa are chasmophytes, which are mainly found on steep calcareous cliffs and in crevices (Georgiou and Delipetrou 2010, Panitsa and Kontopanou 2017). There is a great affinity of endemic chasmophytic plant taxa between the Ionian islands and the neighboring phytogeographical regions of mainland Greece with west-facing coastal areas (Panitsa and Kontopanouh 2017) and endemic plant taxa in the Ionian are expected to be found on the larger and more heterogeneous islands (Iliadou et al. 2014a), such as Kefalonia, Kerkyra, Zakynthos and Lefkada, the higher and most topographically complex islands of the Ionian archipelago. However, the island of Kalamos emerged as a plant diversity hotspot in our study area. More specifically, Kalamos has high α-values for both the total native and the endemic plant taxa. This is not surprising, considering 1) Kalamos' uneven terrain (dominated by 2 mountain ranges with elevation of 677 m and 745 m) mostly covered by calcareous slopes (Baliousis 2015) and 2) its unique phytogeographical position since it is located in close proximity to the most rugged landscape of western Greece.

Our hotspot analysis highlights the important role of small islands in the conservation aspects of the Ionian islands. According to MacArthur and Wilson (1967), below a threshold island area, island species richness apparently varies independently of area. Verifying this 'small island effect', small islands exhibited both lowest and highest diversity values for all diversity metrics and IoE in the Ionian archipelago. Our results indicate four small Ionian islands (i.e. Kalamos, Ereikoussa, Antipaxoi and Atokos) as diversity and/or endemism hotspots. These islands belong to the NATURA 2000 network of protected areas. Consequently, small islands with exceptionally high plant diversity could keep a key role in conservation management plans in the Ionian archipelago.

Conclusions

The minimal isolation/recent formation and the close proximity of the Ionian islands to the mainland source have resulted in islands that still behave as parts of a continuous land mass. The rather reduced dispersal filtering (due to the recent formation of the Ionian islands) have led to islands with homogenized plant communities and to island floras principally comprising common species, also explaining the low proportion of endemics. Finally, our hotspot analysis revealed four small islands with exceptionally high plant diversity, with Kalamos emerging as the most important diversity and endemism hotspot. Our results underline the need to integrate more protected areas into the existing Ionian Management Agencies, in order to achieve an effective management of the priority sites for plant conservation in the Ionian islands.

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Supplementary material (Appendix NJB-02156 at <www.nordicjbotany.org/appendix/njb-02156>). Appendix 1.

Author Queries

JOB NUMBER: 2156
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Q1 There is a mismatch in author names between the reference citation and the list for the reference 'Georgiou and Delipetrou 2010'. Please check.

Q2 There is a mismatch in author names between the reference citation and the list for the reference 'Panitsa and Kontopanouh 2017'. Please check.