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Geography, climate, ecology: What is more important in determining bee diversity in the Aegean Archipelago?

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Abstract

Aim: Understanding which factors drive α - and β -diversity is fundamental to ecological and biogeographical research. Especially in archipelagos, diversity patterns are interesting due to the numerous factors influencing them. Here, we investigate the importance of climate and ecogeographical factors in shaping α - and β -diversity patterns of bee species in the Aegean Archipelago, a bee diversity hotspot.

Location: Nineteen islands in the Aegean Archipelago, located along a N–S climate gradient.

Methods: We systematically sampled the bee fauna of phryganic communities in 100 sites across 19 islands. Using generalized linear models (GLMs), we tested climatic (viz. annual mean temperature and annual precipitation), geographical (island area, proportion of surrounding land mass, distance to climatically similar land mass, and maximum step length of pathway to nearest island/mainland), and ecological parameters (viz. floral abundance) as determinants of bee diversity. Following a multimodel island species–area relationship (ISAR) framework, we ranked islands according to the observed richness to identify biodiversity hotspots. Furthermore, we estimated the effect of the above factors on overall β -diversity as well as on turnover and nestedness components, using multiple regression models on distance matrices.

Results: Island area was the best predictor, positively affecting α -diversity, together with precipitation, surrounding land mass proportion, and floral abundance. Temperature was found to have a significant negative effect on α -diversity. Among all study islands, Samothraki and Kea stood out as bee diversity hotspots, with a bee richness higher than predicted by the multimodel ISAR. The overall β -diversity was mainly driven by the turnover component and positively related to precipitation differences, whereas the nestedness component was positively affected by differences in area and surrounding land mass proportion.

Main conclusion: This study highlights the importance of geography and climate in shaping both α - and β -diversity of bees in the Aegean and suggests that both factors are likely to be crucial for analysing and predicting bee diversity responses to future environmental changes.

KEYWORDS

α -diversity, β -diversity, diversity hotspot, island biogeography, island species–area relationship, nestedness, species composition, species richness, species turnover



1 | INTRODUCTION

Species–area relationships are among the most robust patterns in ecology and biogeography (Lomolino & Weiser, 2001). Although area is generally acknowledged as a powerful explanatory variable for shaping and estimating species richness, it is often considered a surrogate of other factors, such as habitat diversity (e.g., Brose, 2001). Notwithstanding, various models of island species–area relationships (ISARs) have been proposed (see Triantis, Guilhaumon, & Whittaker, 2012; Williams, Lamont, & Henstridge, 2009 for a review) and widely used including for pinpointing biodiversity hotspots (e.g., Fattorini, 2006; Guilhaumon, Gimenez, Gaston, & Mouillot, 2008).

While α -diversity is a measure of species richness in a local assemblage, β -diversity is a measure of variation in assemblage composition among sampling units (Whittaker, 1960). The recent methodological approach of disentangling β -diversity into turnover and nestedness components has been critical in unveiling the causes of β -diversity patterns, as they reflect antithetic ecological processes (Baselga, 2010). Spatial turnover, that is, species replacement among sites, is predicated on mechanisms of environmental filtering or spatial and physical constraints relative to contemporary or historical events (Dapporto, Fattorini, Vodă, Dincă, & Vila, 2014; Leprieur, Olden, Lek, & Brosse, 2009). In contrast, nestedness, that is, differences in species richness, occurs when biotas in species-poor sites are subsets of biotas of species-rich sites (Lomolino, 1996; Wright & Reeves, 1992), mostly due to selective colonization and extinction events, and nested habitats (Ulrich, Almeida-Neto, & Gotelli, 2009; Wang, Bao, Yu, Xu, & Ding, 2010). Nested structure is a common characteristic of insular biotas and has been found to predominate at all spatial scales, from individual islands to entire archipelagos (Sfenthourakis, Giokas, & Tzanos, 2004). It has been linked to colonization ability and migration capacity (Dennis, Hardy, & Dapporto, 2012).

According to the Equilibrium Theory of Island Biogeography (henceforth ETIB), species richness and community assembly are determined by immigration and extinction rates, and the island area and isolation are the synergistic factors that affect these rates (MacArthur & Wilson, 1967). Although this theory satisfactorily explains species richness of insular systems, it suffers limitations, as it ignores additional factors that might enhance or suppress diversity, for example, energy availability (Wright, 1983) or island ontogeny, evolutionary and geological characteristics as formulated by the general dynamic model (GDM) of oceanic island biogeography (Whittaker, Triantis, & Ladle, 2008), which extends the ETIB framework.

Island climate receives a strong oceanic/sea influence, thus, climatic characteristics, such as temperature or precipitation variations along a latitudinal gradient, can be significant for determining insular diversity patterns and species assemblages (Whittaker & Fernandez-Palacios, 2007). Integrating climate into models of global insular species richness has been shown to increase their predictive ability (Cabral, Weigelt, Kissling, & Kreft, 2014; Kalmar & Currie, 2006; Kreft, Jetz, Mutke, Kier, & Barthlott, 2008). Indeed, the effect of climate on species diversity is manifest even within a narrow latitudinal gradient (Petanidou et al., 2018). Geographical factors, such as

geographic distance, are also important in shaping diversity patterns (Diver, 2008). Species richness on islands declines significantly and systematically with the degree of isolation from mainland sources (Dennis, Shreeve, Olivier, & Coutsis, 2000). However, even though distance to mainland constitutes a meaningful measure of isolation and hence island reachability, there are additional, more biologically relevant measures determining isolation, such as the existence of stepping stones, area of surrounding land masses, and distance to climatically similar land masses (Weigelt & Kreft, 2013). Both climate and ecogeographical factors thus strongly affect species richness, but hitherto research has primarily focused on continental areas (e.g., Kivinen, Luoto, Kuussaari, & Helenius, 2006; Stefanescu, Herando, & Páramo, 2004). The importance of both factors in shaping β -diversity patterns and explaining turnover and nestedness components has not been demonstrated until recently (Fattorini & Baselga, 2012; Liu, Dudley, Xu, & Economo, 2017; Svenning, Fløjgaard, & Baselga, 2011). Moreover, it rarely has been investigated on islands (but see Cabral et al., 2014; Hirao, Kubota, & Murakami, 2015).

Due to their unique characteristics, viz. numerous islands of diverse sizes, complex palaeogeographic history, and variable geomorphology, the Aegean islands have become a model region for studying diversity patterns in well-studied taxonomic groups of molluscs, arthropods, and plants (Kallimanis et al., 2010; Kouglioumoutzis et al., 2017; Panitsa, Tzanoudakis, Triantis, & Sfenthourakis, 2006; Pitta, Kassara, Trichas, Sfenthourakis, & Chatzaki, 2017; Sfenthourakis & Panitsa, 2012; Ståhls et al., 2016; Triantis, Sfenthourakis, & Mylonas, 2008; Welter-Schultes & Williams, 1999), but never for bees (see Petanidou et al., 2013). Despite their significant role in providing ecosystem services (viz. pollination of crops and wild plants: Klein et al., 2007; Ollerton, Winfree, & Tarrant, 2011), patterns of bee diversity and related driving factors have only been studied in tropical (e.g., Nemésio & Vasconcelos, 2013; Perillo, Neves, Antonini, & Martins, 2017) and boreal regions (e.g., Kivinen et al., 2006). Thus, the influence of climate and ecogeographical factors on bee species and assemblages at a regional Mediterranean scale, and particularly in the Aegean Archipelago with its outstanding bee species richness (Michener, 1979), remains unexplored.

Based on bees sampled from 19 Aegean islands, this study aims to: (a) explore the combined effect of climate and ecogeographical factors on species richness (α -diversity), (b) estimate species richness and determine the islands performance as bee diversity hotspots, by applying an ISAR multimodel framework (Guilhaumon, Mouillot, & Gimenez, 2010), and (c) identify whether variation in species composition and its components (viz. turnover and nestedness) are driven by climatic and ecogeographical determinants. Based on the ETIB, we hypothesize that α -diversity will be mainly driven by island area. Regarding β -diversity, we expect the community composition to be dominated by the turnover component, considering the high bee faunal variation among islands (Petanidou, unpublished data). Additionally, given the difference in climatic conditions of the study islands arrayed at a latitudinal gradient, we predict climate-related turnover, without pronounced distance effects due to the continental nature of the Aegean islands.

2 | MATERIALS AND METHODS

2.1 | Data collection

We sampled 100 bee communities on 19 islands in the Aegean Archipelago (Figure 1; Appendix S1 in Supporting Information) during the main flowering and bee flight activity period, that is, from March to June over 3 years (2012–2015). To achieve comparable sampling effort per unit area, we aimed for one sampling site per 50 km² island area. However, due to the loss of some sites (destroyed

pantraps caused by grazing animals, wind, or vandalism), this was in a few cases slightly compromised. Three surveys were undertaken at each site: late March to early April, late April to early May, and late May to early June, leaving a minimum of 3 weeks between visits to the same site. We applied the pantrap and hand-netting protocol by Westphal et al. (2008) and Nielsen et al. (2011), modified to efficiently sample the high bee diversity of the Aegean islands. At each site and at each visit, we: (a) used 10 pantrap triplets, each consisting of three UV-bright pantraps of yellow, blue, and white colour; each pantrap was filled with 350 ml of water to which one drop of

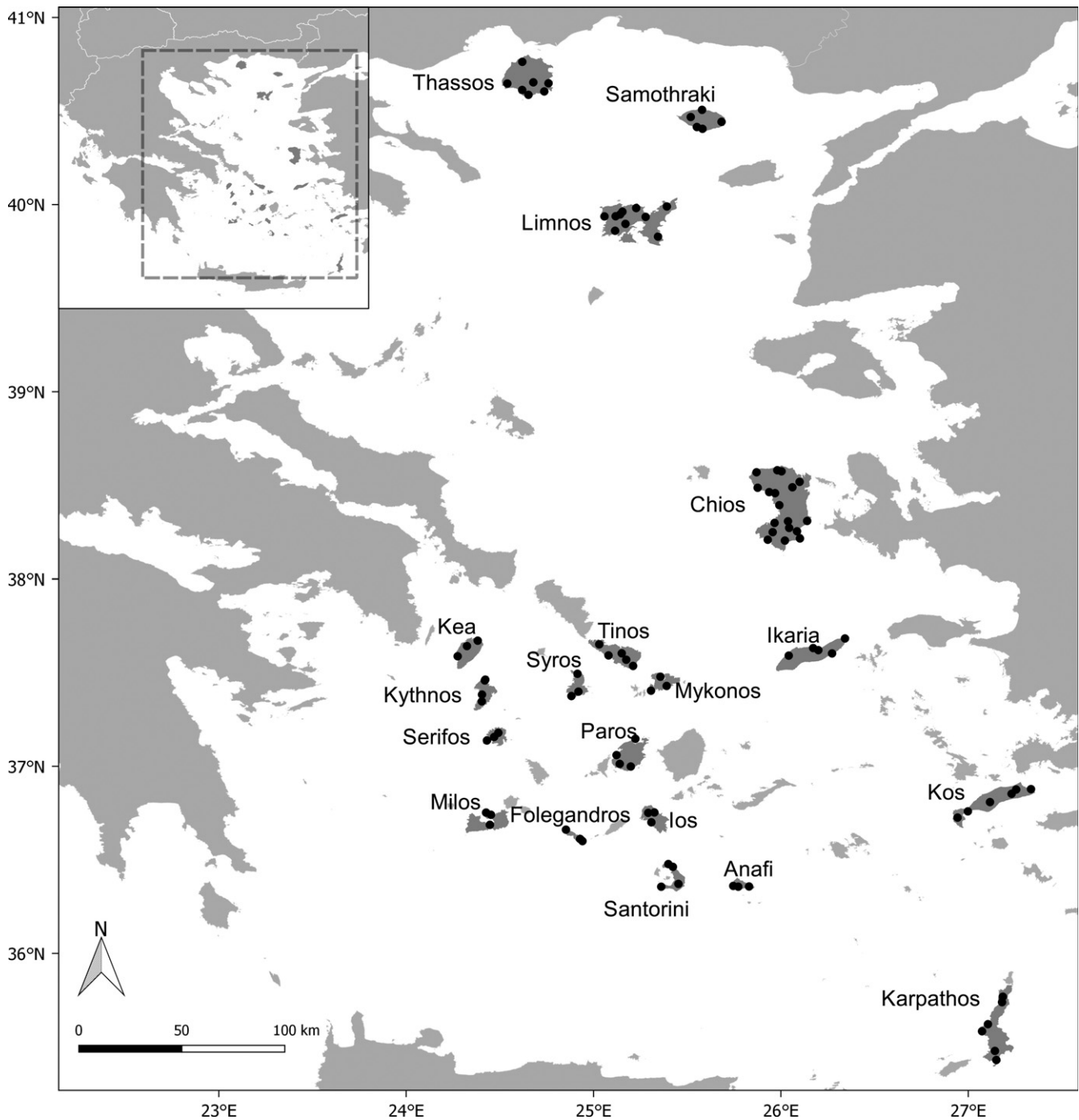


FIGURE 1 The study islands in the Aegean Archipelago. Black dots represent bee sampling sites



aroma-free detergent was added and left onsite to collect for 48 hr; (b) hand-sampled using hand nets for 120 min per site between 10.00 and 16.30 hr, collecting bees observed on flowers along random walks. Bee specimens were identified to species level by European bee taxonomy experts. During each visit, we recorded the total number of functional reproductive units (flowers or inflorescences) of each plant species in 1 m²-squares ($n = 25$) randomly selected within each site.

2.2 | Geographical, climatic, and ecological variables

We selected seven independent variables potentially affecting species richness, belonging to three categories: (a) geographical, accounting for area and isolation, and known to influence island species richness (Kreft et al., 2008; Weigelt & Kreft, 2013): (i) island area (area, in km²), (ii) surrounding land mass proportion (SLMP, in %), (iii) distance to climatically similar largest island/mainland (Dist_{cl}, in km), and (iv) maximum step length from pathway to nearest island/mainland (Dist_{max}, in km); (b) climatic, that is, annual means that have been shown to affect bee richness in the Aegean (Petanidou et al., 2018): (i) annual mean temperature (Temp, in °C) and (ii) annual precipitation (Prec, in mm); and (c) ecological: (i) floral abundance (FIAb), a factor known to act as key determinant of bee communities (Petanidou & Ellis, 1996; Potts et al., 2006).

Island areas and distance metrics were calculated using ArcMap 10.4. Because all sampling sites were located in phryganic (East Mediterranean low scrub) systems, we additionally estimated the area covered by phrygana in each island (see Appendix S2) and performed sensitivity analyses on the GLMs and ISAR models (discussed below), using the total area covered with phrygana, rather than the entire island area, to estimate the reliability of the modelling outputs. SLMP was computed as the proportion of land area surrounding each island; four SLMP indices were tested separately, the percentage of land area within a buffer distance of: (a) 10, (b) 100, (c) 1,000 km, and (d) the sum of these percentages; for SLMP calculations, islands smaller than 1 km² were excluded. Dist_{cl} was computed as the shortest distance from the target island coastline to climatically similar areas ($\pm 5\%$ and $\pm 10\%$ of Temp and Prec, respectively) of mainland or larger source island, whichever was closest. Dist_{max} was defined as maximum inter-island distance derived from minimum inter-island distance path to mainland or larger island of at least double the size of the target island, whichever was closest. The above distance metrics were chosen to represent three different components of isolation (Weigelt & Kreft, 2013). The climatic data were obtained from the EuMedClim database (Fréjaville & Benito Garzón, 2018). For each island, we computed the averaged climatic values over the 30 years preceding the actual sampling year (see Table S3.1 in Appendix S3). After having extracted the climatic data for each site within an island, we assigned their average as the climate data of the island. Floral abundance per island site is given as average floral abundance/m² and was calculated as the sum of abundances over all sites and rounds divided by the number of random plots per site (25) and the number of sites. Based on variance inflation factor

(VIF), multicollinearity among variables was not a concern (VIFs were 1.96–5.42) according to Quinn and Keough (2002). A summary of all variables per island is given in Appendix S3 (see Table S3.2).

2.3 | Calculation of the response variables

α -diversity (species richness) was defined as the number of bee species per island captured by all methods employed. β -diversity was calculated as the compositional dissimilarity between islands using the Sørensen dissimilarity index (β_{sor}) (Baselga, 2010). The β_{sor} was partitioned into two separate components: β_{sim} (turnover), that is, the dissimilarity due to species replacements, and β_{sne} (nestedness), that is, the dissimilarity due to richness differences (Baselga, 2010). Pairwise dissimilarities of the above measures were estimated using the ‘betapart’ R package (Baselga & Orme, 2012).

2.4 | Statistical analysis

2.4.1 | Species richness modelling

To determine the effect of climatic and ecogeographical variables on species richness, we used generalized linear models (GLMs). A Poisson distribution was selected for the dependent variable (count data) and the link function was set to logarithmic. Explanatory variables that were not normally distributed were log₁₀-transformed. All variables were standardized (mean = 0, SD = 1) to improve model convergence. Model selection was performed using the dredge function in ‘MuMIn’ R package (Bartoń, 2016), covering all possible combinations, based on the Akaike's information criterion corrected for small sample sizes (AICc) (but see Harrison et al. [2018] for recent criticism on this approach). To avoid model overfitting, four global models were considered separately, each accounting for one of the four SLMP isolation metrics. Proportion of explained deviance was calculated with the ‘modEVA’ R package (Barbosa, Brown, Jimenez-Valverde, & Real, 2016). Tests using SAM 4.0 (spatial analysis in macroecology, Rangel, Diniz-Filho, & Bini, 2010) revealed that there was no statistically significant spatial autocorrelation in model residuals (see Table S3.3, Figure S3.1 in Appendix S3). To evaluate the relative importance of each of the variables selected by the best GLM model, we performed hierarchical partitioning (Chevan & Sutherland, 1991) using the ‘hier.part’ R package (Walsh & Mac Nally, 2013). The GLMs were also performed with the phryganic area instead of the entire island area.

2.5 | Island species–area relationship

Using the ‘mmSAR’ R package (Guilhaumon et al., 2010), we explored the performance of the following ISAR models: (a) power ($S = cA^z$), (b) exponential ($S = c + z \log(A)$), (c) negative exponential ($S = c(1 - \exp(-zA))$), (d) Monod ($S = (cA)/(z + A)$), (e) rational ($S = (c + zA)/(1 + fA)$), (f) logistic ($S = c/(1 + \exp(-zA + f))$), and (g) cumulative Weibull ($S = c[1 - \exp(-zA^f)]$), where c , z , and f are constant parameters. Since the tested models have different numbers of fitted parameters, they

were evaluated in terms of their performance according to AICc. We used the Akaike weights (w_{AICc}) (i.e., the relative model likelihood given the data) for the estimation of each model's probability to be the best at explaining the data (Burnham & Anderson, 2002). Multimodel inference should be preferred in order to account for the model selection uncertainty in cases that competing models provide similar strength and none of the models fit is strongly supported by the data ($w_i \geq 0.9$) (Burnham & Anderson, 2002). Model averaging was conducted by considering the weighted average of all valid model predictions with respect to model w_{AICc} to construct the multimodel ISAR as: $\hat{S} = \sum_{i=1}^M \hat{S}_i w_i$, where \hat{S} is the multimodel averaged species richness, \hat{S}_i is the species richness inferred from model i , and M is the number of valid models. Confidence intervals (CI) of the multimodel ISAR were devised to take into account uncertainty regarding model selection and parameter estimation by using a non-parametric bootstrapping procedure based on percentile method with 9,999 bootstrap samples (see Guilhaumon et al., 2008). Following Guilhaumon et al. (2008), we ranked islands by positioning the observed richness in the associated vector of bootstrap species richness estimates sorting in ascending order. Islands above the upper limit of the 95% CI of multimodel ISAR are considered relative bee diversity hotspots. The same procedure was repeated when considering phryganic areas alone.

2.5.1 | β -diversity patterns

The relationship between the pairwise compositional dissimilarities (β_{SOR} , β_{SIM} , and β_{SNE}) with pairwise dissimilarities of climatic and eco-geographical variables among islands was estimated by applying multiple regression models on distance matrices (MRM) (Lichstein, 2007). Prior to MRM, we selected distance matrices that had a significant effect on β -diversity indices through simple Mantel tests. These individually significant variables were used in a separate MRM analysis following backward elimination. Simple Mantel tests and MRM analysis were conducted with 9,999 permutations using the 'ecodist' R package (Goslee & Urban, 2007). The dissimilarities of the explanatory variables were expressed as differences (or environmental distances) between pairs of islands using the Euclidean method. Measurements were standardized prior to calculation of dissimilarity matrices. Patterns of pairwise dissimilarity indices (β_{SOR} , β_{SIM} , and β_{SNE}) were described by performing hierarchical clustering using the average linkage method. Dendrograms were visualized and compared using the 'dendextend' R package (Galili, 2015).

We estimated multiple site dissimilarity among all islands, considering the overall β -diversity (β_{SOR}), measured as Sørensen dissimilarity, and the nestedness (β_{SNE}) component, using the 'betapart' R package (Baselga & Orme, 2012), in order to obtain the proportion of nestedness-resultant component with total β -diversity ($\beta_{ratio} = \beta_{SNE}/\beta_{SOR}$). Values less than 0.5 indicate that β -diversity is mainly determined by species turnover, whereas values higher than 0.5 indicate nestedness as the dominant contribution component (Dobrovolski, Melo, Cassemiro, & Diniz-Filho, 2012). Dissimilarity due to nestedness is a related but different concept of nestedness

per se, as it measures the degree of dissimilarity due to a nested pattern and not how perfect the nested pattern is (Baselga, 2010, 2012). Thus, we assessed nestedness of species communities by calculating the nestedness metric based on overlap and decreasing fill (NODF) (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008). The observed NODF value was assessed for statistical significance based on 1,000 simulations of random null communities with the standardized effect size of the observed statistic as z-value. For the construction of the randomized matrices, the quasiswap method was implemented (Miklós & Podani, 2004). The calculation of the NODF metric was performed using the 'vegan' R package (Oksanen et al., 2017). Since we aimed to explore whether islands that support less species richness are subsets of islands richer in species, we evaluated the NODF among islands. All statistical analysis were done in R 3.4.0 (R Core Team, 2017).

3 | RESULTS

A total of 22,047 wild bee specimens (honeybees excluded) belonging to 485 species, 54 genera, and 6 families were sampled on the study islands (see Table S3.1 in Appendix S3). Apidae was the most dominant family (143 species, 17 genera), followed by Megachilidae (120 species, 20 genera), Halictidae (100 species, 9 genera), Andrenidae (90 species, 4 genera), Colletidae (28 species, 2 genera), and Melittidae (4 species, 2 genera).

3.1 | Species richness modelling

Among all candidate models, the one including surrounding land mass area within a 100 km buffer had the lowest AICc (176.86). Neither the distance to climatically similar land mass nor the maximum step length was included in the best-fitting model. The percentage deviance explained by the best-fitting model was 91.16%. The selected variables had a significant effect on species richness ($p < 0.001$, Table 1). Species richness was correlated negatively to annual temperature, but positively to annual precipitation, island area, proportion of land mass within 100 km surrounding a target island, and floral abundance. Hierarchical partitioning revealed that area had a substantially greater independent explanatory power than other variables, followed by proportion of surrounding land mass, annual precipitation, annual temperature, and floral abundance (Figure 2). The GLM results considering the phryganic area alone were similar (cf. Table 1 vs. Table S3.4 in Appendix S3; and Figure 2 vs. Figure S3.2 in Appendix S3).

3.2 | Island species–area relationship

Driven by the importance of island area in affecting species α -diversity, we explored the performance of ISAR models. Overall, the power model had the best fit according to the AICc, followed by the logistic model, while exponential, rational, and Weibull provided the least fit to the data (see Table S3.5 in Appendix S3). However, based



TABLE 1 Regression coefficients \pm SE, the confidence intervals of the regression parameters (lower/upper 95% CI), the z value, and the residual deviances of the generalized linear model relating climatic and geographical variables to bee species richness in the Aegean Archipelago. Temp = mean annual temperature, Prec = annual precipitation, SLMP = proportion of surrounding land mass, Area = entire island area, and FIAb = floral abundance

Variables	Coefficient (\pm SE)	Lower 95% CI	Upper 95% CI	z value	Residual deviance
Intercept	4.46 (\pm 0.03)	4.40	4.50	171.64***	435.59
Temp	-0.10 (\pm 0.03)	-0.16	-0.04	-3.36***	289.40
Prec	0.16 (\pm 0.03)	0.10	0.22	4.91***	160.88
SLMP	0.16 (\pm 0.04)	0.09	0.23	4.25***	133.56
Area	0.30 (\pm 0.03)	0.24	0.37	9.05***	62.92
FIAb	0.18 (\pm 0.04)	0.11	0.25	4.96***	38.52

*** $p < 0.001$.

on AICc weights, none of the models satisfactorily fitted the data ($wAICc < 0.9$ in all models) (see Table S3.5 in Appendix S3), indicating substantial uncertainty regarding model selection. Therefore, islands were ranked according to the CI limits of the averaged ISAR curve. Only Samothraki and Kea scored above the upper 95% CI limit (Figure 3) and are, therefore, considered relative bee diversity hotspots. The sensitivity analysis showed that the above results are robust as the ISAR results considering the phryganic areas alone were equivalent to the ISAR model performance and island ranking using the entire island area (cf. Table S3.5 in Appendix S3 vs. Table S3.6 in Appendix S3; and Figure 3 vs. Figure S3.3 in Appendix S3).

3.3 | β -diversity patterns

The multiple regression analysis on pairwise dissimilarities showed that differences in community composition measured as β_{sor} were significantly positively correlated with differences in annual temperature and precipitation, island area, and surrounding land mass proportions (Table 2). Turnover (β_{sim}) was positively associated with differences in precipitation (although this result should be treated with caution, as precipitation explains little variation in the turnover component); and nestedness-resultant component (β_{sne}) was positively associated with differences in island area and surrounding land mass proportions (Table 2). The dendrogram of the overall pairwise β -diversity pattern showed two distinct clusters, separating islands according to Mid-Aegean Trench, with the exception of Karpathos and Milos; β_{sim} displayed a similarity to the overall pattern, although clusters of highly isolated islands were evident, whereas the nestedness-resultant component differed considerably from the overall pattern, representing the aggregation of islands according to their species richness (see Figure S3.4a–e in Appendix S3). The ratio between the nestedness-resultant and the overall β -diversity was lower than 0.5 ($\beta_{ratio} = 0.09$), signifying the spatial turnover as the prevalent contributor to β -diversity. Bee communities were found to have significant intermediate values of nestedness, since the

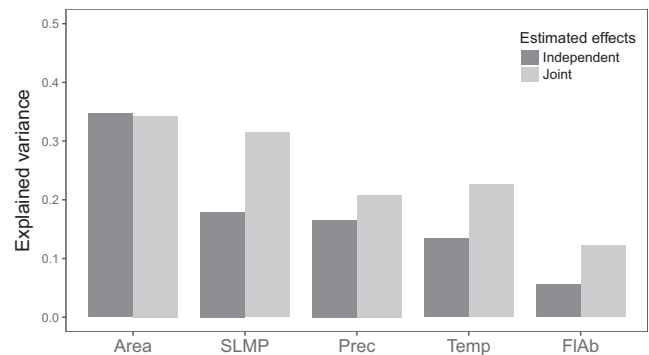


FIGURE 2 Explained variance of the different bee species richness determinants found to be significant, independently or jointly, as estimated from the hierarchical partitioning procedure. They are: entire island area (Area), proportion of surrounding land mass (SLMP), annual precipitation (Prec), annual mean temperature (Temp), and floral abundance (FIAb) of the Aegean islands. Variables are presented in order of total estimated effect. Hierarchical partitioning was implemented with R^2 as a goodness of fit measure

observed NODF for islands was significantly different than expected from the null model ($NODF_{islands} = 53.33$, $z = 4.87$, $p < 0.001$).

4 | DISCUSSION

Island area was the most important factor explaining bee species richness in the Aegean. This is not surprising, as area has been found to drive island species richness in plants and other animal groups within the Archipelago (Fattorini, 2002; Kallimanis et al., 2010; Kougioumoutzis & Tiniakou, 2015; Welter-Schultes & Williams, 1999) and worldwide (Kreft et al., 2008), with larger islands having greater carrying capacity, supporting a diverse number of habitats, and promoting opportunities for within-island speciation.

Surrounding land mass proportion was found to be the best among various isolation metrics explaining the plant diversity in islands at a global scale (Weigelt & Kreft, 2013). The same holds true also for the bee diversity in the Aegean Archipelago, although this metric was also significant at a smaller (100 km) buffer, possibly as a result of the smaller geographical scale of our study. Similarly, Lavery, Olds, Seddon, and Leung (2016) found the percentage of area within a 100 km buffer to influence regional mammalian species richness. Colonization success of bees is expected to depend, among other factors, on the availability of floral abundance, which have been recognized as a structuring element in explaining bee richness at local level (Potts et al., 2006). Interestingly, our results, which consider the phryganic bee richness at the island level, point to the same conclusion. Species exchange in the Aegean may be favoured by the plethora of small islands. Smaller islands can be assumed to comprise habitats less uneven in plant species richness, demonstrating higher plant density and, thus, floral resources, and may positively influence species exchange among islands (Sfenthourakis & Panitsa, 2012). Undoubtedly, species exchange has been much influenced by the Aegean Archipelago's complex geological history (e.g.,

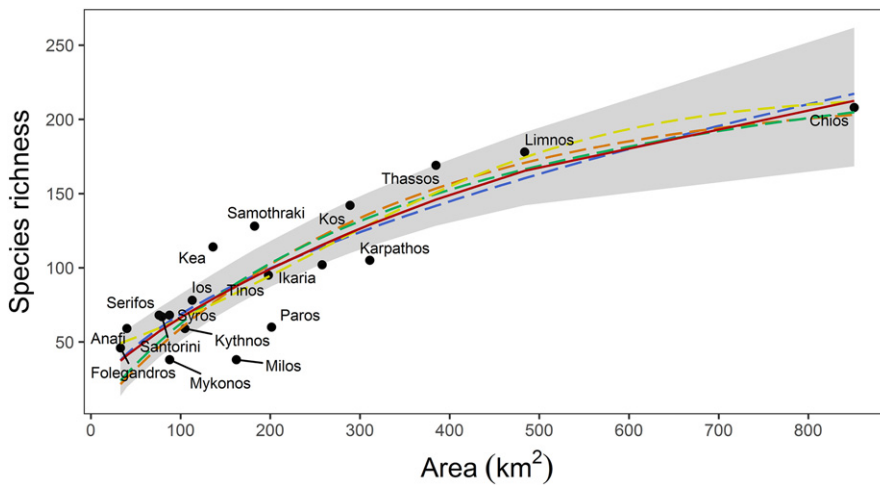


FIGURE 3 Fitting of the ISAR models, based on the entire island area, for bee species richness of the Aegean islands. Broken lines represent the ISAR predictions (blue: power, orange: negative exponential, green: Monod, yellow: logistic). The red solid line represents the averaged multimodel ISAR and the shaded area the 95% nonparametric bootstrap confidence interval. Exponential, rational, and cumulative Weibull are not illustrated as they provided similar results with the above models [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Parameter estimates and p -values from multiple regression models on dissimilarity indices (β_{sor} , β_{sim} , and β_{sne}) of bee species assemblages with differences in environmental variables between the Aegean islands. R^2 values for the entire models are also reported. Significance was assessed by permutation test ($n = 9,999$). Temp = mean annual temperature, Prec = annual precipitation, SLMP = proportion of surrounding land mass and Area = entire island area

β -diversity	Intercept	Temp	Prec	SLMP	Area	R^2
β_{sor}	0.460 ^{ns}	0.020*	0.034***	0.028**	0.028**	0.51***
β_{sim}	0.428 ^{ns}	—	0.023*	—	—	0.05*
β_{sne}	0.046 ^{ns}	—	—	0.024*	0.052***	0.32***

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = nonsignificant.

Messinian Salinity Crisis, Pleistocene changes) (Simaiakis et al., 2017). Indeed, for the Aegean islands, Pleistocene palaeogeography has been identified as a key factor for the present distribution patterns (Fattorini, 2002; Poulakakis et al., 2014) and Pleistocene distances as the drivers of its current biota (Hausdorf & Hennig, 2005).

Temperature has a negative effect on bee species richness in the Aegean, a result consistent with Hamblin, Youngsteadt, and Frank (2018) regarding bee abundance, and Stefanescu et al. (2004) regarding butterfly diversity. Although these areas exhibit different climatic regimes (temperate and Mediterranean, respectively), their findings are convergent and contradict the results reported by Kivinen et al. (2006) who, in boreal landscapes, found a positive effect of temperature on multispecies richness, including bees, implying that temperature is a limiting factor in higher latitudes versus water availability as a limiting factor in the Mediterranean Region. Given that the Aegean is a relatively summer-dry area, our finding that precipitation has a positive effect on bee diversity in the Aegean is not surprising: bee richness is maximal in areas where water availability, a resource regulated by the interplay between temperature (energy) and precipitation (water), is adequate. The above results agree with Petanidou et al. (2018) who found that pollinator species richness in the Aegean Archipelago depends positively on annual precipitation, and the conclusions by Hawkins et al. (2003), who reviewed published studies at broader scales, and argued that in cool climates, invertebrate species richness is strongly affected by energy, that is, temperature, whereas in warmer climates, it is affected by water availability

alone or combined with energy. Our findings, although at smaller extent, fit well in the above context, demonstrating that bee richness is controlled by water–energy interaction, either directly or via flowering plant abundance. Thus, bee richness is probably related to more diverse floral resources (mainly nectar) available within the better rainfed habitats of the generally hot and dry Archipelago (Petanidou, Goethals, & Smets, 1999; Petanidou & Smets, 1996; Takkis, Tscheulin, & Petanidou, 2018; Takkis, Tscheulin, Tsalkatis, & Petanidou, 2015).

Species richness was modelled as a function of area, without the effect of the remaining variables, using nonlinear regressions. Based on area alone, Samothraki and Kea stood out as islands with higher than expected species richness. Both islands, together with Thassos, ranked at the upper limit of the multimodel CI; all three were connected to the mainland during Pleistocene, thus, likely to have faced many colonizations and extinctions. The islands of the central Cyclades, together with Icaria and Karpathos, were probably invaded by fewer species during Pleistocene as shown elsewhere (cf. Triantis & Mylonas, 2009), which might explain the lower than expected species richness of these islands. Southern Cyclades appear at the upper part of the curve, perhaps due to their geological and plant diversity, that is, ecological features that make these islands particularly attractive for bees. Indeed, Anafi has been demonstrated to be a plant diversity hotspot in the southern Aegean (Kougioumoutzis & Tiniakou, 2015), which the authors attributed to its plant diversity vis-à-vis geological diversity. Kos, ranked at the highest CI limit of the



multimodel curve, was an exception among the eastern Aegean islands. The proximity of Kos to Anatolian coast facilitates species migration and probably reflects the palaeogeographic history of the Aegean. During mid-Pleistocene, Kos, as well as Chios, was connected to Asia Minor (Sakellariou & Galanidou, 2016; Triantis & Mylonas, 2009), allowing unhindered migration and colonization. During that period, Limnos was only connected to the nearby islands, implying some isolation from the continental area, probably resulting in only moderate colonization.

In the Aegean islands, β -diversity of bees seems to be driven by differences in temperature, precipitation, proportion of surrounding land mass, and area. The significant correlation with climate can be explained with the existence of climatic gradient across our study islands. For instance, our results differ from those found by Hausdorf and Hennig (2005) that annual temperature and precipitation, with the exception of the negative impact of annual precipitation on reptiles, did not significantly influence the faunal composition of various animal groups, that is, snails, isopods, beetles, and butterflies, in the central Aegean islands. This might reflect the homogeneous climate regime within the Cyclades compared to our study area, that is, the entire Aegean.

The lack of distance effects on turnover component could be explained by the relative short inter-island distances in the Aegean, at least compared to interconnected oceanic insular systems where turnover has been found to be driven by isolation effects (Cabral et al., 2014; Carvalho & Cardoso, 2014). This is especially true for the Cycladic islands, which due to having experienced several historical connections and detachments share a higher number of species and consequently show higher levels of nestedness (Fattorini, 2007).

The positive effect of area differences in nestedness-resultant component reveals the trend that communities of smaller islands tend to be subsets of larger islands (Lomolino, 1996), probably resulting from a selective extinction mechanism, as increased area differences promote extinction rates and lead to nested patterns (Wright, Patterson, Mikkelsen, Cutler, & Atmar, 1998). Nestedness, despite the different area requirements of species, may be further associated with species differences in dispersal ability (Wang et al., 2010). For instance, Carvalho and Cardoso (2014) found that it was the area mainly important for the assemblage composition of Macaronesian spiders with increased mobility. The authors stressed the likelihood that dispersal limitation affects island community composition in response to island area. This finding might explain the clusters of highly isolated islands, Paros–Limnos and Karpathos–Milos, which perhaps share good colonists from the same species pool.

Bee community assemblages were found to be driven by turnover in species composition, which is reflected in the steeper ISAR curve, and might be associated with long-term speciation events and the existence of Pleistocene refugia (Baselga, Lobo, Svenning, Aragón, & Araújo, 2012; Fattorini & Baselga, 2012; Hortal et al., 2011) or dispersal barriers, such as the Mid-Aegean Trench, ultimately resulting in different species composition between the Cycladic and the Anatolian island groups (Ståhls et al., 2016). The significant intermediate levels of nestedness can be explained by the continental

character of most island groups and their common palaeogeographic history (Kougioumoutzis, Simaiakis, & Tiniakou, 2014; Sfenthourakis & Triantis, 2017) that influences ecological processes, such as selective immigration and extinction (Wright et al., 1998).

5 | CONCLUSIONS

Most of the variables investigated as potential factors driving natural and ecological processes related to species dispersal and island species richness colonization rate were significant. Our results showed an increased probability of colonization on larger islands, influenced by the degree of isolation, climate, and to a lesser extent floral abundance. However, we did not find exclusive area effects, as many smaller islands exhibit higher number of species than predicted by their size. Although species turnover among islands was significant, overall we conclude that the Aegean seems to be characterized by both species turnover and nestedness. Prospective conservation perspectives need to capture this by utilising different implementation strategies. The geoecological complexity of the Aegean and the scarcity of bee diversity studies suggest that more research, controlling for the impact of historical and human-mediated factors, could provide further elucidation of bee diversity patterns beyond the findings of this study.

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REFERENCES

- Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117, 1227–1239. <https://doi.org/10.1111/j.0030-1299.2008.16644.x>
- Barbosa, A. M., Brown, J. A., Jimenez-Valverde, A., & Real, R. (2016). modEVA: Model Evaluation and Analysis. R package version 1.3.2. <https://CRAN.R-project.org/package=modEVA>

- Bartoń, K. (2016). MuMIn: Multi-Model Inference. R package version 1.15.6. <https://CRAN.R-project.org/package=MuMIn>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21, 1223–1232. <https://doi.org/10.1111/j.1466-8238.2011.00756.x>
- Baselga, A., Lobo, J. M., Svenning, J. C., Aragón, P., & Araújo, M. B. (2012). Dispersal ability modulates the strength of the latitudinal richness gradient in European beetles. *Global Ecology and Biogeography*, 21, 1106–1113. <https://doi.org/10.1111/j.1466-8238.2011.00753.x>
- Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Brose, U. (2001). Relative importance of isolation, area and habitat heterogeneity for vascular plant species richness of temporary wetlands in east-German farmland. *Ecography*, 24, 722–730. <https://doi.org/10.1034/j.1600-0587.2001.240610.x>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer-Verlag.
- Cabral, J. S., Weigelt, P., Kissling, W. D., & Kreft, H. (2014). Biogeographic, climatic and spatial drivers differentially affect α -, β - and γ -diversities on oceanic archipelagos. *Proceedings of the Royal Society B*, 281, 20133246. <https://doi.org/10.1098/rspb.2013.3246>
- Carvalho, J. C., & Cardoso, P. (2014). Drivers of beta diversity in Macaronesian spiders in relation to dispersal ability. *Journal of Biogeography*, 41, 1859–1870. <https://doi.org/10.1111/jbi.12348>
- Chevan, A., & Sutherland, M. (1991). Hierarchical partitioning. *The American Statistician*, 45, 90–96.
- Dapporto, L., Fattorini, S., Vodá, R., Dincă, V., & Vila, R. (2014). Biogeography of western Mediterranean butterflies: Combining turnover and nestedness components of faunal dissimilarity. *Journal of Biogeography*, 41, 1639–1650. <https://doi.org/10.1111/jbi.12315>
- Dennis, R. L. H., Hardy, P. B., & Dapporto, L. (2012). Nestedness in island faunas: Novel insights into island biogeography through butterfly community profiles of colonization ability and migration capacity. *Journal of Biogeography*, 39, 1412–1426. <https://doi.org/10.1111/j.1365-2699.2012.02698.x>
- Dennis, R. L. H., Shreeve, T. G., Olivier, A., & Coutsis, J. G. (2000). Contemporary geography dominates butterfly diversity gradients within the Aegean archipelago (Lepidoptera: Papilionoidea, Hesperioidea). *Journal of Biogeography*, 27, 1365–1383. <https://doi.org/10.1046/j.1365-2699.2000.00514.x>
- Diver, K. C. (2008). Not as the crow flies: Assessing effective isolation for island biogeographical analysis. *Journal of Biogeography*, 35, 1040–1048.
- Dobrovolski, R., Melo, A. S., Cassemiro, F. A. S., & Diniz-Filho, J. A. F. (2012). Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 21, 191–197. <https://doi.org/10.1111/j.1466-8238.2011.00671.x>
- Fattorini, S. (2002). Biogeography of the tenebrionid beetles (Coleoptera, Tenebrionidae) on the Aegean Islands (Greece). *Journal of Biogeography*, 29, 49–67. <https://doi.org/10.1046/j.1365-2699.2002.00656.x>
- Fattorini, S. (2006). Detecting biodiversity hotspots by species–area relationships: A case study of Mediterranean beetles. *Conservation Biology*, 20, 1169–1180. <https://doi.org/10.1111/j.1523-1739.2006.00418.x>
- Fattorini, S. (2007). Non-randomness in the species–area relationship: Testing the underlying mechanisms. *Oikos*, 116, 678–689.
- Fattorini, S., & Baselga, A. (2012). Species richness and turnover patterns in European tenebrionid beetles. *Insect Conservation and Diversity*, 5, 331–345. <https://doi.org/10.1111/j.1752-4598.2011.00164.x>
- Fréjaville, T., & Benito Garzón, M. (2018). The EuMedClim Database: Yearly climate data (1901–2014) of 1 km resolution grids for Europe and the Mediterranean Basin. *Frontiers in Ecology and Evolution*, 6, 31. <https://doi.org/10.3389/fevo.2018.00031>
- Galili, T. (2015). dendextend: An R package for visualizing, adjusting and comparing trees of hierarchical clustering. *Bioinformatics*, 31, 3718–3720. <https://doi.org/10.1093/bioinformatics/btv428>
- Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, 22, 1–19.
- Guilhaumon, F., Gimenez, O., Gaston, K. J., & Mouillot, D. (2008). Taxonomic and regional uncertainty in species–area relationships and the identification of richness hotspots. *Proceedings of the National Academy of Sciences USA*, 105, 15458–15463. <https://doi.org/10.1073/pnas.0803610105>
- Guilhaumon, F., Mouillot, D., & Gimenez, O. (2010). mmSAR: An R-package for multimodel species–area relationship inference. *Ecography*, 33, 420–424.
- Hamblin, A. L., Youngsteadt, E., & Frank, S. D. (2018). Wild bee abundance declines with urban warming, regardless of floral density. *Urban Ecosystems*, 21, 419–428. <https://doi.org/10.1007/s11252-018-0731-4>
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., ... Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 6, e4794. <https://doi.org/10.7717/peerj.4794>
- Hausdorf, B., & Hennig, C. (2005). The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. *Biological Journal of the Linnean Society*, 84, 785–795. <https://doi.org/10.1111/j.1095-8312.2005.00467.x>
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J. F., Kaufman, D. M., ... Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117. <https://doi.org/10.1890/03-8006>
- Hirao, T., Kubota, Y., & Murakami, M. (2015). Geographical patterns of butterfly species diversity in the subtropical Ryukyu Islands: The importance of a unidirectional filter between two source islands. *Journal of Biogeography*, 42, 1418–1430. <https://doi.org/10.1111/jbi.12501>
- Hortal, J., Diniz-Filho, J. A. F., Bini, L. M., Rodríguez, M. Á., Baselga, A., Nogués-Bravo, D., ... Lobo, J. M. (2011). Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, 14, 741–748. <https://doi.org/10.1111/j.1461-0248.2011.01634.x>
- Kallimanis, A. S., Bergmeier, E., Panitsa, M., Georghiou, K., Delipetrou, P., & Dimopoulos, P. (2010). Biogeographical determinants for total and endemic species richness in a continental archipelago. *Biodiversity and Conservation*, 19, 1225–1235. <https://doi.org/10.1007/s10531-009-9748-6>
- Kalmar, A., & Currie, D. J. (2006). A global model of island biogeography. *Global Ecology and Biogeography*, 15, 72–81. <https://doi.org/10.1111/j.1466-822X.2006.00205.x>
- Kivinen, S., Luoto, M., Kuussaari, M., & Helenius, J. (2006). Multi-species richness of boreal agricultural landscapes: Effects of climate, biotope, soil and geographical location. *Journal of Biogeography*, 33, 862–875. <https://doi.org/10.1111/j.1365-2699.2006.01433.x>
- Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B*, 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Kougioumoutzis, K., Simaiakis, S. M., & Tiniakou, A. (2014). Network biogeographical analysis of the central Aegean archipelago. *Journal of Biogeography*, 41, 1848–1858. <https://doi.org/10.1111/jbi.12342>
- Kougioumoutzis, K., & Tiniakou, A. (2015). Ecological factors driving plant species diversity in the South Aegean Volcanic Arc and other central



- Aegean islands. *Plant Ecology & Diversity*, 8, 173–186. <https://doi.org/10.1080/17550874.2013.866989>
- Kougoumoutzidis, K., Valli, A. T., Georgopoulou, E., Simaiakis, S. M., Triantis, K. A., & Trigas, P. (2017). Network biogeography of a complex island system: The Aegean Archipelago revisited. *Journal of Biogeography*, 44, 651–660. <https://doi.org/10.1111/jbi.12920>
- Kreft, H., Jetz, W., Mutke, J., Kier, G., & Barthlott, W. (2008). Global diversity of island floras from a macroecological perspective. *Ecology Letters*, 11, 116–127.
- Lavery, T. H., Olds, A. D., Seddon, J. M., & Leung, L. K.-P. (2016). The mammals of northern Melanesia: Speciation, ecology, and biogeography. *Mammal Review*, 46, 60–76. <https://doi.org/10.1111/mam.12057>
- Leprieur, F., Olden, J. D., Lek, S., & Brosse, S. (2009). Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. *Journal of Biogeography*, 36, 1899–1912. <https://doi.org/10.1111/j.1365-2699.2009.02107.x>
- Lichstein, J. W. (2007). Multiple regression on distance matrices: A multivariate spatial analysis tool. *Plant Ecology*, 188, 117–131. <https://doi.org/10.1007/s11258-006-9126-3>
- Liu, C., Dudley, K. L., Xu, Z. H., & Economo, E. P. (2017). Mountain metacommunities: Climate and spatial connectivity shape ant diversity in a complex landscape. *Ecography*, 40, 1–11.
- Lomolino, M. V. (1996). Investigating causality of nestedness of insular communities: Selective immigrations or extinctions? *Journal of Biogeography*, 23, 699–703. <https://doi.org/10.1111/j.1365-2699.1996.tb00030.x>
- Lomolino, M. V., & Weiser, M. D. (2001). Towards a more general species-area relationship: Diversity on all islands, great and small. *Journal of Biogeography*, 28, 431–445. <https://doi.org/10.1046/j.1365-2699.2001.00550.x>
- MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton: Princeton University Press.
- Michener, C. D. (1979). Biogeography of the bees. *Annals of the Missouri Botanical Garden*, 66, 277–347. <https://doi.org/10.2307/2398833>
- Miklós, I., & Podani, J. (2004). Randomization of presence-absence matrices: Comments and new algorithms. *Ecology*, 85, 86–92. <https://doi.org/10.1890/03-0101>
- Nemésio, A., & Vasconcelos, H. L. (2013). Beta diversity of orchid bees in a tropical biodiversity hotspot. *Biodiversity and Conservation*, 22, 1647–1661. <https://doi.org/10.1007/s10531-013-0500-x>
- Nielsen, A., Steffan-Dewenter, I., Westphal, C., Messinger, O., Potts, S. G., Roberts, S. P. M., ... Petanidou, T. (2011). Assessing bee species richness in two Mediterranean communities: Importance of habitat type and sampling techniques. *Ecological Research*, 26, 969–983. <https://doi.org/10.1007/s11284-011-0852-1>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... Wagner, H. (2017) vegan: Community Ecology Package. R package version 2.4-3. <https://CRAN.R-project.org/package=vegan>
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Panitsa, M., Tzanoudakis, D., Triantis, K. A., & Sfenthourakis, S. (2006). Patterns of species richness on very small islands: The plants of the Aegean archipelago. *Journal of Biogeography*, 33, 1223–1234. <https://doi.org/10.1111/j.1365-2699.2006.01481.x>
- Perillo, L. N., Neves, F. S., Antonini, Y., & Martins, P. (2017). Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient. *PLoS ONE*, 12, e0182054. <https://doi.org/10.1371/journal.pone.0182054>
- Petanidou, T., & Ellis, W. N. (1996). Interdependence of native bee faunas and floras in changing Mediterranean communities. In A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, & I. H. Williams (Eds.), *The conservation of bees* (pp. 201–226). London: Academic Press.
- Petanidou, T., Goethals, V., & Smets, E. (1999). The effects of nutrient and water availability on nectar secretion and nectary structure of the dominant Labiatae species of phrygana. *Systematics and Geography of Plants*, 68, 233–244. <https://doi.org/10.2307/3668604>
- Petanidou, T., Kallimanis, A. S., Lazarina, M., Tscheulin, T., Devalez, J., Stefanaki, A., ... Sgardelis, S. P. (2018). Climate drives plant–pollinator interactions even along small-scale climate gradients: The case of the Aegean. *Plant Biology*, 20, 176–183. <https://doi.org/10.1111/plb.12593>
- Petanidou, T., & Smets, E. (1996). Does temperature stress induce nectar secretion in Mediterranean plants? *New Phytologist*, 133, 513–518. <https://doi.org/10.1111/j.1469-8137.1996.tb01919.x>
- Petanidou, T., Ståhls, G., Vujić, A., Olesen, J. M., Rojo, S., Thrasylvoulou, A., ... Tscheulin, T. (2013). Investigating plant–pollinator relationships in the Aegean: The approaches of the project POL-AEGIS (The pollinators of the Aegean archipelago: Diversity and threats). *Journal of Apicultural Research*, 52, 106–117. <https://doi.org/10.3896/IBRA.152.2.20>
- Pitta, E., Kassara, C., Trichas, A., Sfenthourakis, S., & Chatzaki, M. (2017). Community variation of spiders, beetles and isopods in three small island groups of the Aegean Sea: The interplay between history and ecology. *Journal of Biogeography*, 44, 1077–1087. <https://doi.org/10.1111/jbi.12979>
- Potts, S. G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A., & Willmer, P. (2006). Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. *Biological Conservation*, 129, 519–529. <https://doi.org/10.1016/j.biocon.2005.11.019>
- Poulakakis, N., Kapli, P., Lymberakis, P., Trichas, A., Vardinoyiannis, K., Sfenthourakis, S., & Mylonas, M. (2014). A review of phylogeographic analyses of animal taxa from the Aegean and surrounding regions. *Journal of Zoological Systematics and Evolutionary Research*, 53, 18–32.
- Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511806384>
- R Core Team (2017) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <https://www.r-project.org/>
- Rangel, T. F., Diniz-Filho, J. A. F., & Bini, L. M. (2010). SAM: A comprehensive application for Spatial Analysis in Macroecology. *Ecography*, 33, 46–50. <https://doi.org/10.1111/j.1600-0587.2009.06299.x>
- Sakellariou, D., & Galanidou, N. (2016). Pleistocene submerged landscapes and Palaeolithic archaeology in the tectonically active Aegean region. In J. Harff, G. Bailey, & F. Lüth (Eds.), *Geology and archaeology: Submerged landscapes of the continental shelf* (pp. 145–178). Geological Society, Special Publications 411, London.
- Sfenthourakis, S., Giokas, S., & Tzanatos, E. (2004). From sampling stations to archipelagos: Investigating aspects of the assemblage of insular biota. *Global Ecology and Biogeography*, 13, 23–35. <https://doi.org/10.1111/j.1466-882X.2004.00065.x>
- Sfenthourakis, S., & Panitsa, M. (2012). From plots to islands: Species diversity at different scales. *Journal of Biogeography*, 39, 750–759. <https://doi.org/10.1111/j.1365-2699.2011.02639.x>
- Sfenthourakis, S., & Triantis, K. A. (2017). The Aegean archipelago: A natural laboratory of evolution, ecology and civilisations. *Journal of Biological Research-Thessaloniki*, 24, 1–13.
- Simaiakis, S. M., Rijdsdijk, K. F., Koene, E. F. M., Norder, S. J., Van Boxel, J. H., Stocchi, P., ... Tjørve, E. (2017). Geographic changes in the Aegean Sea since the Last Glacial Maximum: Postulating biogeographic effects of sea-level rise on islands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 471, 108–119. <https://doi.org/10.1016/j.palaeo.2017.02.002>
- Ståhls, G., Vujić, A., Petanidou, T., Cardoso, P., Radenković, S., Ačanski, J., ... Rojo, S. (2016). Phylogeographic patterns of *Merodon* hoverflies in the Eastern Mediterranean region: Revealing connections and barriers. *Ecology and Evolution*, 6, 2226–2245. <https://doi.org/10.1002/ece3.2021>
- Stefanescu, C., Herrando, S., & Páramo, F. (2004). Butterfly species richness in the north-west Mediterranean Basin: The role of natural and human-induced factors. *Journal of Biogeography*, 31, 905–915. <https://doi.org/10.1111/j.1365-2699.2004.01088.x>



- Svenning, J. C., Fløjgaard, C., & Baselga, A. (2011). Climate, history and neutrality as drivers of mammal beta diversity in Europe: Insights from multiscale deconstruction. *Journal of Animal Ecology*, *80*, 393–402. <https://doi.org/10.1111/j.1365-2656.2010.01771.x>
- Takkis, K., Tscheulin, T., & Petanidou, T. (2018). Differential effects of climate warming on the nectar secretion of early- and late-flowering Mediterranean plants. *Frontiers in Plant Science*, *9*, 874. <https://doi.org/10.3389/fpls.2018.00874>
- Takkis, K., Tscheulin, T., Tsalkatis, P., & Petanidou, T. (2015). Climate change reduces nectar secretion in two common Mediterranean plants. *AoB PLANTS*, *7*, plv111. <https://doi.org/10.1093/aobpla/plv111>
- Triantis, K. A., Guilhaumon, F., & Whittaker, R. J. (2012). The island species-area relationship: Biology and statistics. *Journal of Biogeography*, *39*, 215–231. <https://doi.org/10.1111/j.1365-2699.2011.02652.x>
- Triantis, K. A., & Mylonas, M. (2009). Greek islands, biology. In R. G. Gillespie & D. Glague (Eds.), *Encyclopedia of islands* (pp. 388–392). Berkeley, CA: University of California Press.
- Triantis, K. A., Sfenthourakis, S., & Mylonas, M. (2008). Biodiversity patterns of terrestrial isopods from two island groups in the Aegean Sea (Greece): Species–area relationship, small island effect, and nestedness. *Ecoscience*, *15*, 169–181. <https://doi.org/10.2980/15-2-3065>
- Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. *Oikos*, *118*, 3–17. <https://doi.org/10.1111/j.1600-0706.2008.17053.x>
- Walsh, C., & Mac Nally, R. (2013). hier.part: Hierarchical Partitioning. R package version 1.0-4. <https://CRAN.R-project.org/package=hier.part>
- Wang, Y., Bao, Y., Yu, M., Xu, G., & Ding, P. (2010). Nestedness for different reasons: The distributions of birds, lizards and small mammals on islands of an inundated lake. *Diversity and Distributions*, *16*, 862–873. <https://doi.org/10.1111/j.1472-4642.2010.00682.x>
- Weigelt, P., & Kreft, H. (2013). Quantifying island isolation - insights from global patterns of insular plant species richness. *Ecography*, *36*, 417–429. <https://doi.org/10.1111/j.1600-0587.2012.07669.x>
- Welter-Schultes, F. W., & Williams, M. R. (1999). History, island area and habitat availability determine land snail species richness of Aegean islands. *Journal of Biogeography*, *26*, 239–249. <https://doi.org/10.1046/j.1365-2699.1999.00276.x>
- Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., ... Steffan-Dewenter, I. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, *78*, 653–671. <https://doi.org/10.1890/07-1292.1>
- Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*, 279–338. <https://doi.org/10.2307/1943563>
- Whittaker, R. J., & Fernandez-Palacios, J. M. (2007). *Island biogeography: Ecology, evolution, and conservation*. Oxford, UK: Oxford University Press.
- Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, *35*, 977–994. <https://doi.org/10.1111/j.1365-2699.2008.01892.x>
- Williams, M. R., Lamont, B. B., & Henstridge, J. D. (2009). Species–area functions revisited. *Journal of Biogeography*, *36*, 1994–2004. <https://doi.org/10.1111/j.1365-2699.2009.02110.x>

- Wright, D. H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, *41*, 496–506. <https://doi.org/10.2307/3544109>
- Wright, D. H., Patterson, B. D., Mikkelsen, G. M., Cutler, A., & Atmar, W. (1998). A comparative analysis of nested subset patterns of species composition. *Oecologia*, *113*, 1–20.
- Wright, D. H., & Reeves, J. H. (1992). On the meaning and measurement of nestedness of species assemblages. *Oecologia*, *92*, 416–428. <https://doi.org/10.1007/BF00317469>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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