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Spatial patterns of genus-level phylogenetic endemism in the tree flora of Mediterranean Europe

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Abstract

Aim: The Mediterranean Basin is a major hotspot of plant biodiversity, including forest trees. Over the past centuries, Mediterranean forests have been fragmented and over-exploited, to which the threats of climate change are now added. Our aim is to better understand patterns and processes of tree biodiversity in the Mediterranean and to provide indicators complementing the traditional approaches to biodiversity conservation based on species counts and occurrences, using georeferenced phylogenetic diversity and endemism analyses in a spatial ecological context.

Location: Mediterranean Europe.

Methods: Using a dated phylogeny of the 64 Euro-Mediterranean tree genera, we calculated phylogenetic diversity for all 50 × 50 km² grid cells spanning Mediterranean Europe ($n = 643$) and compared values with those obtained for genus-level taxonomic diversity. Then, we tested the relative influence of geography, past and present climate, and soil on tree diversity (phylogenetic or taxonomic) and its geographical turnover. Geographical patterns of phylogenetic endemism were inferred using the Categorical Analyses of Neo- and Paleo-Endemism (CANAPE) methodology.

Results: We showed that phylogenetic and taxonomic diversity within and among cells are correlated and influenced by soil parameters as well as current, Holocene and Late Glacial Maximum climate. Southern Spain, Cyprus and some Aegean islands contained areas of disproportionately high phylogenetic diversity and a concentration of phylogenetic paleo-endemics, while phylogenetic neo-endemism was high in eastern Sicily. Mixed phylogenetic endemism regions were detected in southern Spain and Portugal, in the Balkans and in Crete.

Main conclusions: Our phylogenetic approach provides relevant indicators for better protecting forests of the Mediterranean, encompassing past and present evolutionary processes and factors. We consider areas that show a concentration of evolutionary history manifested by high phylogenetic endemism as high priority targets for the conservation of the European tree flora.

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KEYWORDS

conservation, Euro-Mediterranean vascular flora, Nonmetric Multidimensional Scaling, phylogenetic diversity, phylogenetic endemism, relative environmental turnover

1 | INTRODUCTION

Forests and woodlands harbour immense terrestrial and aquatic biodiversity and represent one of the most species-rich habitat type worldwide (Gibson et al., 2011; Lindenmayer, 2009). Forests provide a wide range of critically important ecosystem services such as climate regulation, biomass production, water supply and purification, pollination, and provision of habitats for forest species (Brockhoff et al., 2013; Decocq et al., 2016; Liang et al., 2016; Mori et al., 2017; Thompson et al., 2011). Over the last centuries, forest habitats have been destroyed at rates much higher than ever observed in human history (Gaston, 2000; Johnson et al., 2017; Turvey & Crees, 2019). As a result, a high number of species have become extinct and/or suffered severe population declines (Mace et al., 2005), with many advancing at high speed to higher categories of threat every year, notably in the biodiversity hotspots of the world (Hoffmann et al., 2010; Le Roux et al., 2019). The forests of the Mediterranean Basin, a recognized hotspot of biodiversity, follow the same trend (Gauquelin et al., 2018; Médail & Quézel, 1997).

Where and how to prioritize biodiversity conservation is a key political, societal and scientific issue for modern societies. Traditionally, biodiversity assessments have been based on species counts, valuing areas in terms of species richness and number of endemics and/or threatened species, mostly per spatial units (Kier et al., 2009; Myers et al., 2000; Norman, 2003). However, as species richness, endemism and threat can be influenced by many factors, such as the species concepts and taxonomic standards used, the spatial scale and the intensity of the sampling. Using such data can thus make biodiversity assessments and comparisons across taxonomic groups and sites limited in scope or misleading (Hillebrand et al., 2018; McKerrow et al., 2018; Van Jaarsveld et al., 1998). Limitations may also arise when considering all species equal entities and ignoring their particular functional role in the ecosystem, their associated communities and/or their evolutionary history (e.g., Doxa et al., 2020).

The contribution of phylogenetic systematics to the biodiversity conservation debate stems from the very idea that species are not equivalent entities from an evolutionary point of view (Mishler, 2009). As tools to characterize species in terms of evolutionary history using DNA sequences became increasingly available, phylogenetic diversity (PD), the sum of branch lengths in a phylogeny connecting a set of taxa, was proposed as a measure to quantify the loss of evolutionary history (Faith, 1992; Nipperess et al., 2012). A major advantage of PD is that it is relatively resistant to changes in taxonomic status (not that we expect any here, as the genus-level taxonomy of Mediterranean trees is well known and accepted, see Médail et al., 2019) and, thus, allows direct comparisons among different taxonomic groups. Additionally, PD can be also

compared with other diversity measurements, such as functional diversity, including the role of evolutionary history in assembly rules in communities. For instance, facilitation-mediated coexistence has been demonstrated to be driven by evolutionary history of interacting species (Valiente-Banuet & Verdú, 2007), as the functional syndromes of Mediterranean woody plants (Herrera, 1992; Verdú & Pausas, 2013) or the different niche response to fire in communities (Ojeda et al., 2010).

Phylogeny-based methods for measuring biodiversity have developed rapidly during the last decades, with one important area of development relating to endemism (Rosauer et al., 2009). Endemism has always been a major consideration in biogeography and one of the most important criteria when defining conservation priorities (Bacchetta et al., 2012; Linder, 2001). The concept of endemism is implicitly and closely related to the idea of irreplaceability (Margules & Pressey, 2000), and therefore of conservation value. However, the traditional definition of endemism has been narrowly interpreted as the complete restriction of a taxon to a certain area (i.e. absolute endemism). Relative endemism, which refers to the degree of restriction of taxon-range on a quantitative scale ranging from 1 (absolute endemism) to 0 (ubiquitous), broadens the concept (Crisp et al., 2001). In order to integrate evolutionary information, the concept of relative endemism has been extended to the geographic restriction of clades at any taxonomic level, a metric called phylogenetic endemism (PE, Mishler et al., 2014; Rosauer et al., 2009).

Phylogenetic diversity and endemism are most often used to characterize alpha diversity (PD or PE) of given local sites. When entire geographical areas are considered, these estimators can be complemented by the quantification of phylogenetic beta diversity, that is, the turnover in PD among local sites (Graham & Fine, 2008). This estimator is similar to traditional measures of species turnover among sites with the exception that it refers to the shared and unshared branches of the phylogeny that are measured instead of the shared and unshared species. Turnover can also be measured for PE, by weighting range-restricted branches more heavily than common branches, and is termed "phylogenetic range weighted turnover" (Laffan et al., 2016). All these measurements can enhance our understanding of biodiversity patterns and can be used for conservation assessment and planning (Thornhill et al., 2016).

The Mediterranean biome worldwide contains *circa* 20% of the world's floristic richness on only 2% of its terrestrial surface (Médail & Quézel, 1997). Many biogeographical and phylogenetic studies have been conducted in the five Mediterranean climate regions of the world to elucidate the composition and structure of their floras (e.g., Rundel et al., 2016). Comprehensive biome-wide phylogenetic surveys are also available for South Africa (Forest et al., 2007),

California (Kling et al., 2019; Thornhill et al., 2017), Chile (Morlon et al., 2011; Scherson et al., 2017) and Australia (Mishler et al., 2014). Although many studies of the biodiversity of the Mediterranean Basin exist (Médail et al., 2019; Thompson, 2020), surprisingly, a comprehensive spatial phylogeny is still lacking for this region, by far the largest Mediterranean climate region in the world and the second-largest terrestrial biodiversity hotspot of the world (Myers et al., 2000). Only spatially restricted phylogenies are available, notably in southern Spain (Molina-Venegas et al., 2015; Simon-Porcar et al., 2018). The most comprehensive phylogeny available to date for the region is the dated phylogeny at genus level for all tree taxa of the Euro-Mediterranean region of Cheikh Albassatneh et al. (2020).

Here, we combine the genus-level phylogeny of Cheikh Albassatneh et al. (2020) with the most exhaustive compilation of occurrence data for these tree genera across the European part of the Mediterranean Basin (Médail et al., 2019; Monnet et al., 2020). Our specific goal was to single out regions of high phylogenetic neo- and paleo-endemism, thereby increasing our knowledge of biodiversity spatial patterns and of the ecological factors that can explain their emergence, as well as contributing to prioritizing areas of high conservation value. For this aim, we (a) calculated a series of taxonomic and phylogenetic diversity indices for each of the 50×50 km grid cells ($n = 643$) covering the entire European part of the Mediterranean Basin; (b) quantified among-cell variation and identified the main environmental factors explaining genus turnover and (c) calculated grid cell level phylogenetic endemism indicators using the Categorical Analyses of Neo- and Paleo-Endemism (CANAPE) methodology.

2 | MATERIAL AND METHODS

2.1 | Study area

Our study area is the Euro-Mediterranean-region defined by Médail et al. (2019), the North Mediterranean terrestrial ecoregion in the biogeographic classification scheme of Olson et al. (2001). These biogeographical limits of the Euro-Mediterranean region are similar to those proposed by Médail and Quézel (1997), except for some mountain ridges in the Italian peninsula and the Balkans. The total area covered, including islands, is 1,610,200 km², with a coastline approximately 45,200 km in length. The orographic variation in the area is large and elevations range from 0 metres above sea level (m.a.s.l.) up to 3,482 m a.s.l. (Mulhacén, Sierra Nevada, Spain).

Following the biogeographic delineation of Europe of Rivas-Martínez et al. (2004), our study area comprises fifteen biogeographical provinces (Figure 1), covering in parts or in total the following countries, from west to east: Portugal, Spain, France, Italy, Malta, Slovenia, Croatia, Montenegro, Albania, Macedonia, Greece and Cyprus.

2.2 | Data sources for tree occurrences, environmental variables and the phylogeny

The woody vegetation of the Mediterranean is made of diverse types of shrublands (maquis, garrigue, phrygana) and forests, where tree morphology varies widely with environmental

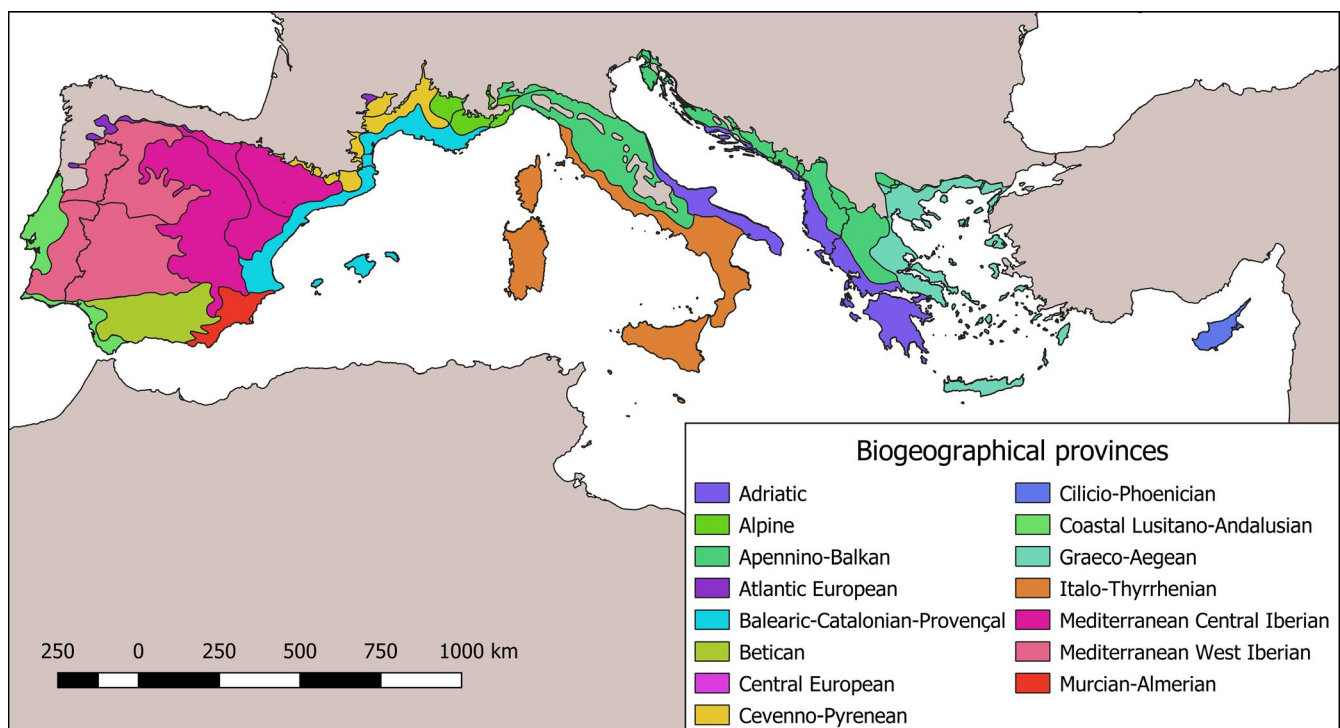


FIGURE 1 Distribution of the 15 biogeographical provinces (sensu Rivas-Martínez et al., 2004) of the Euro-Mediterranean region

constraints (climate, geology, geomorphology, soil type), habitat types and anthropogenic activities. We adopted the criteria elaborated by Médail et al. (2019) concerning tree definition and used their checklist of 64 native tree genera. For genus occurrence and their spatial distribution, we used the data compiled by Monnet et al. (2020).

We used a total of 643 grid cells of 50×50 km spatial resolution to completely cover the European Mediterranean Basin. The database of tree genus occurrence within each cell can be found in Appendix S1. The spatial resolution of environmental variables was originally 344 km^2 for current climate and paleoclimate data (WORLDCLIM, <https://worldclim.org/>) and 250 km^2 for soil data (SOILGRIDS, <https://soilgrids.org/>). To match our genus occurrence data, environmental data were aggregated to a $2,500 \text{ km}^2$ spatial resolution (50×50 km) using the package raster (Hijmans et al., 2015) so as to obtain one average value per cell. For our analysis, we used 30 different environmental variables (Appendix S2) which are further described below.

We used the dated genus-level phylogenetic tree of Cheikh Albassatneh et al. (2020). This phylogeny was built using sequence data of three chloroplast DNA regions commonly used for phylogenetic and taxonomic barcoding purposes: the protein-coding *rbcl* and *matK* genes, and the non-coding intergenic spacer *trnH-psbA* (Hollingsworth et al., 2009; Kress & Erickson, 2007). The number of concatenated sites added up to 1,759 base pairs. The chronogram of Cheikh Albassatneh et al. (2020) is timed in million years and its topology and branch lengths are constrained using multiple calibration points. This phylogeny is largely congruent with the most recent Angiosperm Phylogeny Group classification (APGIV, Chase et al., 2016). Using a chronogram instead of a non-dated phylogeny makes it possible to account for the slow mutation rate of plastid DNA and reduces the risk of not detecting the most recent phylogenetic endemism centres.

2.3 | Relative environmental turnover—diversity among cells and correlation with the environment

To quantify among-cell variation and identify the main environmental factors explaining genus turnover, we estimated beta pairwise diversity using the *betapart* package in R (Baselga, 2012) and the following decomposition based on Sørensen's metric: $\beta_{\text{sor}} = \beta_{\text{sim}} + \beta_{\text{sne}}$, where β_{sor} is the total beta diversity, β_{sim} is beta turnover and β_{sne} is beta nestedness. This decomposition can be adapted to the calculation of beta taxonomic and phylogenetic diversities. We first computed incidence-based pairwise dissimilarities for the beta taxonomic (composition) diversity. The *beta.pair* function estimates three distance matrices: (a) turnover (replacement), (b) nestedness and (c) total dissimilarity (the sum of both components). We then computed pairwise phylogenetic dissimilarities for beta phylogenetic diversity, using the *phylo.beta.pair* function which similarly estimates three distance matrices: (a)

phylogenetic turnover, (b) phylogenetic nestedness and (c) the sum of both values.

Phylogenetic dissimilarities are based on Faith's phylogenetic diversity. For our analyses, we retained Simpson's beta turnover dissimilarity index (β_{sim}) as the most relevant. Contrary to nestedness, spatial turnover implies the replacement of some taxa by others as a consequence of environmental sorting or spatial and historical constraints (Qian et al., 2005), our focus in this study. β_{sim} values were in a matrix format (pairwise distance matrix of dissimilarities) for the 643 grid cells covering the Euro Mediterranean area. The relationships between β_{sim} taxonomic and phylogenetic matrices were explored using Mantel tests and 999 permutations (Mantel, 1967). The diversity indices of the few cells that had a surface area less than $2,500 \text{ km}^2$ (border cells) were calculated in the same way as those of the other cells. The spatial coordinates of a cell were those of its centroid.

Relative environmental turnover (RET) was applied to examine the relationship between environmental variables and the tree genera of the Euro-Mediterranean area, using phylogenetic and taxonomic (composition) turnover (González-Orozco et al., 2016). As with previous studies (Buckley & Jetz, 2008), we used the term environmental turnover to explore rates of change of dissimilarity by taxonomic replacement in Mediterranean tree genera and their relationship to the environment depending on geographical distances.

Then, we employed the β_{sim} matrix to compute Nonmetric Multidimensional Scaling using the metaMDS method implemented in the R *vegan* packages (Oksanen et al., 2012). The metaMDS method performs Nonmetric Multidimensional Scaling (NMDS), a reduced representation rank-order ordination, and tries to find a stable solution using several random starts. In addition, it standardizes the scaling in the result, so that the configurations are easier to interpret, and adds taxa scores to the grid cell ordination. We reduced the number of dimensions to two axes, as recommended. We then fitted the environmental vectors onto the β_{sim} ordination using the vector fitting *envfit* function of the *vegan* package in R (Oksanen et al., 2012).

The environmental variables that best explained the patterns of turnover were then displayed as vectors only for the cases with high predictability ($p < .001$), assessed by 999 permutations. The "stress" values of the *envfit* results were used to estimate the efficiency of the NMDS ordinations. Stress values represent the difference between distances in the reduced, two-axis dimension compared with the original complete multidimensional space. Stress values >0.05 provide an excellent reduced dimension representation of turnover, values >0.1 a great representation, values >0.2 a good representation, while values >0.3 provide a poor representation. The values of each grid cell along the first and second axes of the NMDS ordination of β_{sim} distances were extracted and mapped into five arbitrary classes (that kept the number of cells per class as balanced as possible while emphasizing differences for easy visualization) over the study area using *Quantum GIS* (QGIS Development Team, 2014). NMDS values that are very different indicate strong differences in cell diversity.

All environmental variables used are described in Appendix S3. All computations and analyses were performed using the R statistical environment (R Core Team, 2018).

2.4 | Phylogenetic diversity and endemism analyses

Rao's phylogenetic diversity coefficient was calculated using the *ade4* packages in R (Thioulouse et al., 1997). *Biodiverse* v.2.99 (Laffan et al., 2010) was used to calculate a set of six other diversity indices and associated randomizations for our 643 equal-area square grid cells (50 × 50 km) covering the Euro-Mediterranean area. These were as follows: Taxonomic Richness (TR), Weighted Endemism (WE; Crisp et al., 2001), Phylogenetic Diversity (PD; Faith, 1992), Phylogenetic Endemism (PE; Rosauer et al., 2009), Relative Phylogenetic Diversity (RPD; Mishler et al., 2014), Relative Phylogenetic Endemism (RPE; Mishler et al., 2014). RPE was then employed to calculate a set of four phylogenetic endemism indices using the Categorical analysis of neo- and paleo-endemism (CANAPE; Mishler et al., 2014) method.

Taxonomic richness (TR) is defined as the number of taxa observed in each cell of the grid. Weighted Endemism (WE; Crisp et al., 2001; Laffan & Crisp, 2003; Laffan et al., 2013) is a range-weighted richness score, where the contribution of each taxon is weighted by its respective full geographic range in the European Mediterranean. Phylogenetic Diversity (PD; Faith, 1992) and Phylogenetic Endemism (PE; Rosauer et al., 2009) are the phylogenetic equivalents of TR and WE, respectively. PD is calculated as the sum of the branch lengths (from root to tips) of all the taxa observed in each cell whereas PE is the sum of branch lengths weighted by the full geographic range of the taxon. Branch lengths are proportional to time as the phylogeny used is time-calibrated. Relative Phylogenetic Diversity (RPD) and Relative Phylogenetic Endemism (RPE) are calculated as the ratios between the PD and PE obtained from the original tree and a reference tree with the same topology but with all branches of equal length (Mishler et al., 2014).

Grid cells were assessed for their phylogenetic endemism using CANAPE (Mishler et al., 2014). CANAPE is a two-step process that assesses the contribution to PE from branches that are longer or shorter than expected, for locations that are first shown to be significantly high or low in PE. The process then assesses the significance of the RPE. All cells significant for one of these tests are classified into four non-overlapping categories (González-Orozco et al., 2016; Mishler et al., 2014; Thornhill et al., 2016): (a) cells corresponding to centres of paleo-endemism (few taxa with long branches, significantly high RPE), (b) cells corresponding to centres of neo-endemism (few taxa with short branches, significantly low RPE), (c) cells corresponding to mixed-endemism (rare long and rare short branches, not significant for RPE but significant denominator and significant numerator, p -value < .05) and (iv) cells corresponding to centres of super-endemism (rare long and rare short branches, not significant for RPE but significant

denominator and significant numerator, p -value < .01). In all cases, endemism is meant at genus level.

The significance of the observed PD, PE, RPD and RPE values was assessed using non-parametric tests based on a random reassignment of all the taxa into the grid cells. The distribution of the expected values of these indices under the null hypothesis was calculated from 999 trials of the randomization procedure. Indices in the highest 2.5% or the lowest 2.5% of the distribution were considered significant (two-tailed test).

For calculating the relationship between diversity indices and environmental factors, we used the factorial design of the PCA using the *FactoMineR* packages in R (Lê et al., 2008) and matrix of Spearman's Rank correlation coefficient using the *Hmisc* packages in R (Harrell & Harrell, 2019). We also calculated the relationship between the five CANAPE categories (neo-endemism, paleo-endemism, mixed-endemism, super-endemism, not significant) and the geographical and environmental variables which showed significant influence on indices of alpha diversity: longitude (Coords_X), latitude (Coords_Y), Last Glacial Maximum (LGM) maximum temperature (Tmax_LGM), Last Inter-Glacial precipitation (P_LIG), Mid-Holocene maximum temperature (Tmax_mid_H), solar radiation (SRAD) and current temperature variables (Tavg, Tmax and Tmin) (Appendix S3) overlapped with the five categories of the CANAPE results. As normality of the residuals (one of the fundamental assumptions for ANOVAs) was not fulfilled for the three comparisons (results not shown), we used a non-parametric Kruskal-Wallis test. If at least one of the distributions was significantly different from the others (p < .05), then Wilcoxon pairwise comparisons (two-tailed tests with Holm's correction) were performed to disentangle which categories were significantly different from each other (p < .05). The comparison was plotted using the method of Kassambara (2017).

Groups of cells showing significant PE using CANAPE were identified using an agglomerative UPGMA cluster analysis in *Biodiverse* v.2.99 (Laffan et al., 2010), and the range-weighted phylogenetic turnover metric (Laffan et al., 2016). By focusing on the shared range-restricted branches, this analysis highlights geographic regions within which the evolutionary makeup of the endemic flora is relatively homogeneous (Link-Pérez & Laffan, 2018; Thornhill et al., 2017).

3 | RESULTS

3.1 | Taxonomic and phylogenetic beta turnover—biodiversity among cells and correlation with environmental factors

There was a highly significant relationship between the beta turnover taxonomic diversity and beta turnover Faith's phylogenetic diversity (Mantel test, observation = 0.8920115, simulated p value = .01). Figure 2 shows the results of the beta turnover phylogenetic diversity NMDS analysis plotted over the map of our study area. The coordinates of the NMDS axes were aggregated into five

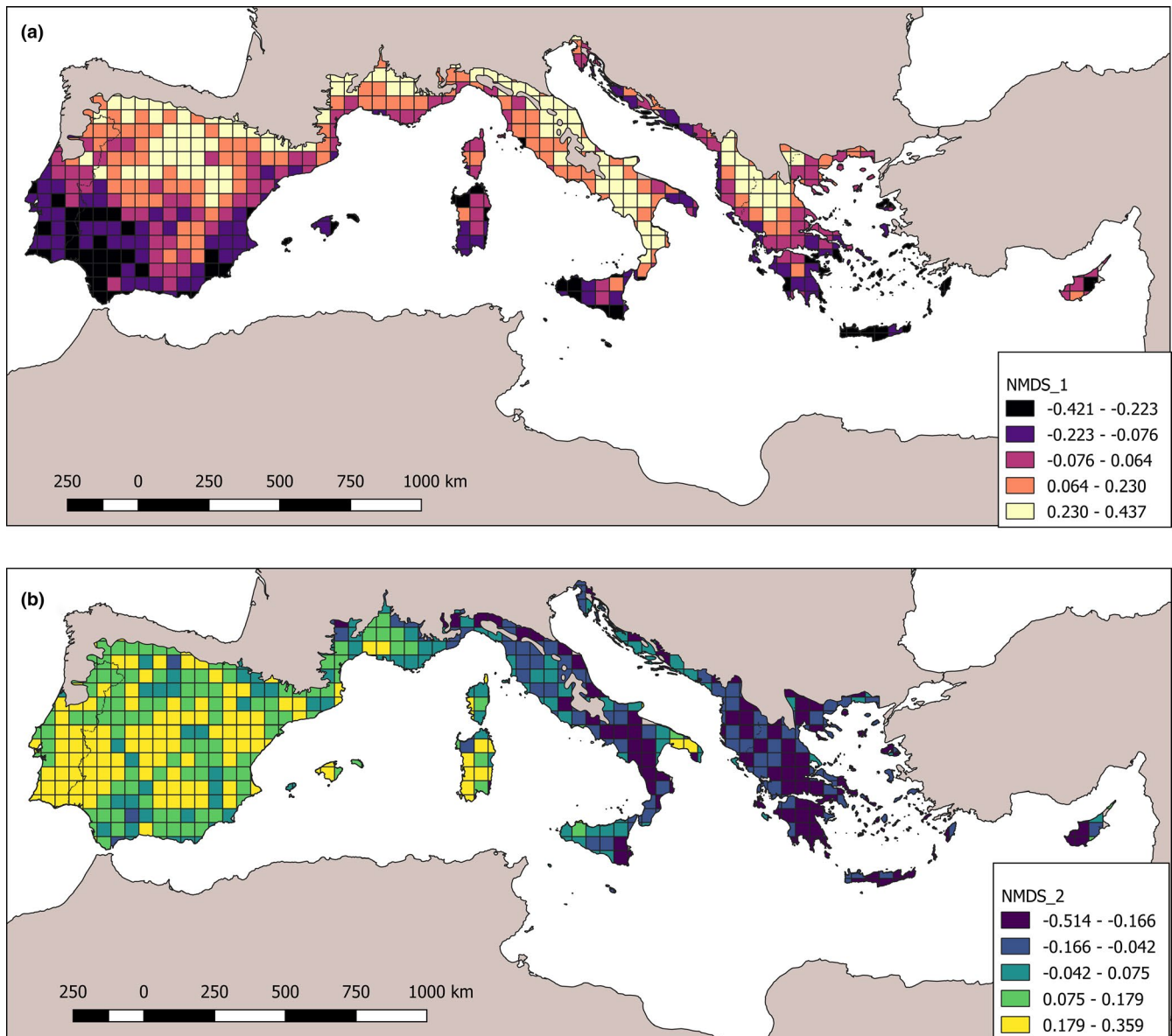


FIGURE 2 Phylogenetic turnover of Euro-Mediterranean tree genera measured using the non-metric multidimensional scaling (NMDS) method of (a) axis 1 (NMDS1) and (b) axis 2 (NMDS2). Colours indicate ranges of coordinates on the NMDS axes and were kept different for axes 1 and 2 as they cover different ranges on the two different axes

classes (see Appendix S4 for the number of cells per NMDS class). Cells with the highest and lowest NMDS values indicate regions with high genus turnover.

Particularly, Figure 2a shows that cells with high NMDS scores (light yellow cells) are located mostly in the Northern Mediterranean region, while cells with low NMDS scores (black cells) are mostly in the Southern Mediterranean and in islands. In Figure 2b, featuring NMDS axis 2, high-value NMDS scores (yellow cells) are mostly in the Western Mediterranean region while low-value NMDS scores (black cells) are mostly in the Eastern Mediterranean.

The scores of the two NMDS axes that characterize phylogenetic turnover could be explained with a moderately good fit (stress value of 0.2749) by different environmental variables. The NMDS plot (Appendix S5) and the table of environment vectors (Appendix S6)

show the relationship between the beta turnover phylogenetic diversity and the environmental variables.

Areas of either high- or low-NMDS values indicate regions with high genus turnover, whereas NMDS values close to zero indicate regions with the lowest genus turnover. The largest positive values of the NMDS axis 1 (light yellow squares in Figure 2a) were associated with Last Glacial Maximum precipitation (P_LGM), texture class (Texture_0.30), derived available soil water capacity (DASWC_30) and depth to bedrock (DBR_200), which corresponded to cells from the northern parts of the two Iberian biogeographic provinces, from the northern Cevenno-Pyrenean and Alpine provinces and the Apennino-Balkan province (Figures 1 and 2a; Appendix S5). The largest negative values of the NMDS axis 1 (black squares in Figure 2a) were associated with Mid-Holocene

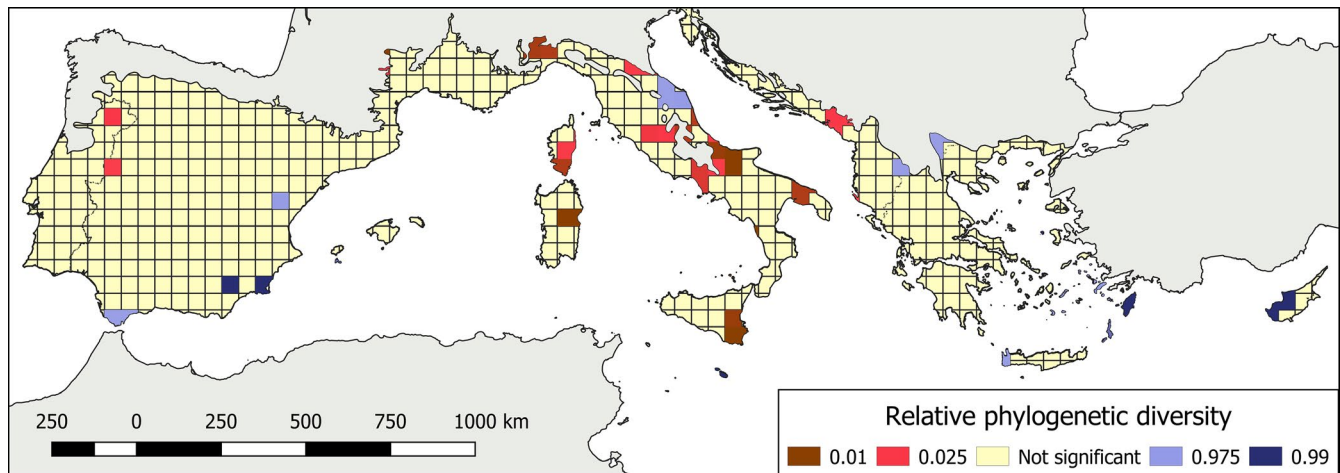


FIGURE 3 Map of the relative phylogenetic diversity (RPD) significance in Mediterranean Europe. Areas in blue have a concentration of significantly longer branches than expected; whereas, areas in red have a concentration of significantly shorter branches than expected

minimum temperature and precipitations ($T_{min_mid_H}$ and P_{mid_H}), current average, minimum and maximum temperature (T_{avg} , T_{min} and T_{max}) and clay content ($ClayCMFD_{0.30}$), which corresponded to cells from the Betican and Murcian-Almerian provinces, the southern Graeco-Aegean province and most of the large islands (Figures 1 and 2a; Appendix S5).

The largest positive values of the NMDS axis 2 (bright yellow squares in Figure 2b) were associated with sand content ($SandCMF_{0.30}$) and texture class ($Texture_{0.30}$), which corresponded to cells from most of the provinces of the Iberian Peninsula. The largest negative values of the NMDS axis 2 (dark purple squares in Figure 2b) were associated with Last Inter-Glacial minimum and maximum temperature (T_{min_LIG} and T_{max_LIG}), Last Inter-Glacial precipitation (P_{LIG}), water vapour pressure (WVP), cation exchange capacity of soil ($CECSoil_{0.30}$) and wind speed (WS), which corresponded to cells from most of the Central and Eastern Mediterranean provinces (Central Italy, Balkans and Cyprus) (Figures 1 and 2b; Appendix S5).

3.2 | Phylogenetic diversity and environmental drivers

The Spearman's Rank correlation coefficient (Appendix S7) and factorial design of the PCA (Appendix S8) showed a positive relationship between PD, TR, and Rao phylogenetic diversity and the following variables (Appendix S3): annual precipitation (P), soil organic carbon ($SoilOCST_{0.15-30}$), coarse fragments volume at depth 0.30 m ($CFV_{0.30}$), silt content at depth 0.30 m ($SiltMF_{0.30}$) and Last Glacial Maximum precipitation (mm/Years) (P_{LGM}). The extreme scattered points associated with these vectors are situated in the north and centre of Greece. On the other hand, the relationship between PD, TR and Rao phylogenetic diversity was negative with the solar radiation variables ($kJ\ m^{-2}\ day^{-1}$; SRAD), Last Glacial Maximum temperature variables (T_{min_LGM} and T_{max_LGM}), Mid-Holocene

temperature variables ($T_{min_mid_H}$ and $T_{max_mid_H}$) and current maximum temperature (T_{max}).

The contribution of PE to the first axes of the PCA is relatively low (Appendix S8). Relationships between PE and environmental variables appear on the 1–4 PCA plane (Appendix S8). PE correlates positively with the Mid-Holocene precipitation (P_{mid_H}), and negatively with silt content at depth 0.30 m ($SiltMF_{0.30}$).

All biodiversity indices were significantly correlated (Appendix S7). However, while TR was highly significantly related to PD ($r = .97$; Appendix S9a) without scatter (as in our beta diversity analysis), PE was less significantly related to PD ($r = .45$; Appendix S9b), and with high scatter, indicating that PE adds information to an analysis only focusing on TR (also see the maps of TR, PD, PE, PWE and Rao in Appendix S10).

3.3 | Categorical analysis of neo- and paleo-endemism (CANAPE)

Relative phylogenetic diversity divided the study area into three broad parts (Figure 3). In its western part, significantly high RPD indicating a concentration of long phylogenetic branches was found in the south of Iberian Peninsula while significantly low RPD, indicating a concentration of short phylogenetic branches, was found in the north of Iberian Peninsula (north-eastern Portugal). In its central part, significantly high RPD was in the north-eastern Italian Peninsula while significantly low RPD was in the islands (Sicily, Sardinia and Corsica) and the edges of the Italian Peninsula. In its eastern part, significantly high RPD was scattered in the north of the Balkan Peninsula and the islands of Crete and Cyprus.

The CANAPE analysis identified 76 cells of high phylogenetic endemism (22 paleo-endemism, 10 neo-endemism, 40 mixed-endemism and 4 super-endemism cells) in Mediterranean Europe. Areas dominated by paleo-endemism were in south-eastern Spain as well as in the islands of Psara and Rhodes in Greece and in

Cyprus (Figure 4). The areas dominated by neo-endemism were mostly located in eastern Sicily while the areas dominated by super-endemism were scattered within few cells at the margins of the study area, in southern Portugal, in south-eastern Italy, in south-western Croatia and in the Greek Islands of Samothraki and the Cyclades (Naxos, Keros, Amorgòs, Santorini and Anafi). The areas dominated by mixed-endemism were located at the eastern and western edges of our study area, in the southern and western regions of the Iberian Peninsula, in the Belasica Mountains of Bulgaria and Greece, and in Crete (more details in Appendix S10). Contributions from genera such as *Juniperus*, *Chamaerops* and *Tetraclinis* in the Iberian Peninsula, *Liquidambar*, *Cupressus*, *Phoenix*, *Pyrus* and *Ceratonia* in Greece, *Acer*, *Cedrus*, *Cupressus*, *Quercus* and *Sorbus* in Cyprus and *Zelkova*, *Genista*, *Cytisus* and *Chamaerops* in Sicily may explain at least in part the phylogenetic endemism structures observed.

Several environmental variables could explain the distribution of the CANAPE categories of endemism (Figure 5; Appendices S11 and S12). Latitude (Coords_Y) and longitude (Coords_X) were correlated to paleo and mixed phylogenetic endemism, with many cells in either category located in southern islands and in either the Iberian or the Balkan Peninsula. Paleo-endemism was more frequent in cells with relatively high LGM and mid-Holocene maximum temperature (Tmax_LGM and Tmax_Mid_H), while mixed and neo-endemism cells were grouped in the areas of low Tmax_LGM. Current minimum temperature (T_{min}) positively affected the distribution of Paleo and neo-endemism. Paleo-endemism was also more frequent in cells with relatively high Late Inter-Glacial precipitation (P_LIG). Paleo-endemism cells were in the areas of the highest solar radiation

(SRAD), in contrast to mixed and neo-endemism cells which were grouped in the areas of low SRAD.

The range-weighted phylogenetic turnover analysis showed that the greatest dissimilarity was observed between the coast of the southern and western Iberian Peninsula, north-eastern Sicily and Crete, and the rest of the Euro-Mediterranean region which formed a discrete cluster (Figure 6).

4 | DISCUSSION

4.1 | Taxonomic diversity, phylogenetic diversity and environmental factors

Our results demonstrate a strong overall congruence between phylogenetic diversity (sensu Faith, 1992) and taxonomic richness of the genera of European Mediterranean trees. Although there is an expected congruence between phylogenetic and taxonomic diversity overall, strong spatial congruence is often rare because the shape of phylogenetic trees results from evolutionary processes that are not accounted for at taxonomic levels and because locally, taxonomic assemblages result from non-random ecological processes acting on regional pools (Cadotte & Tucker, 2018).

Our analysis also highlighted areas of high beta turnover taxonomic diversity (and thus of high beta turnover phylogenetic diversity) within biogeographic provinces and pointed out the environmental factors that could explain their spatial structure. While the high diversity of the southernmost and northernmost cells of our study area were correlated with many relatively recent (Holocene

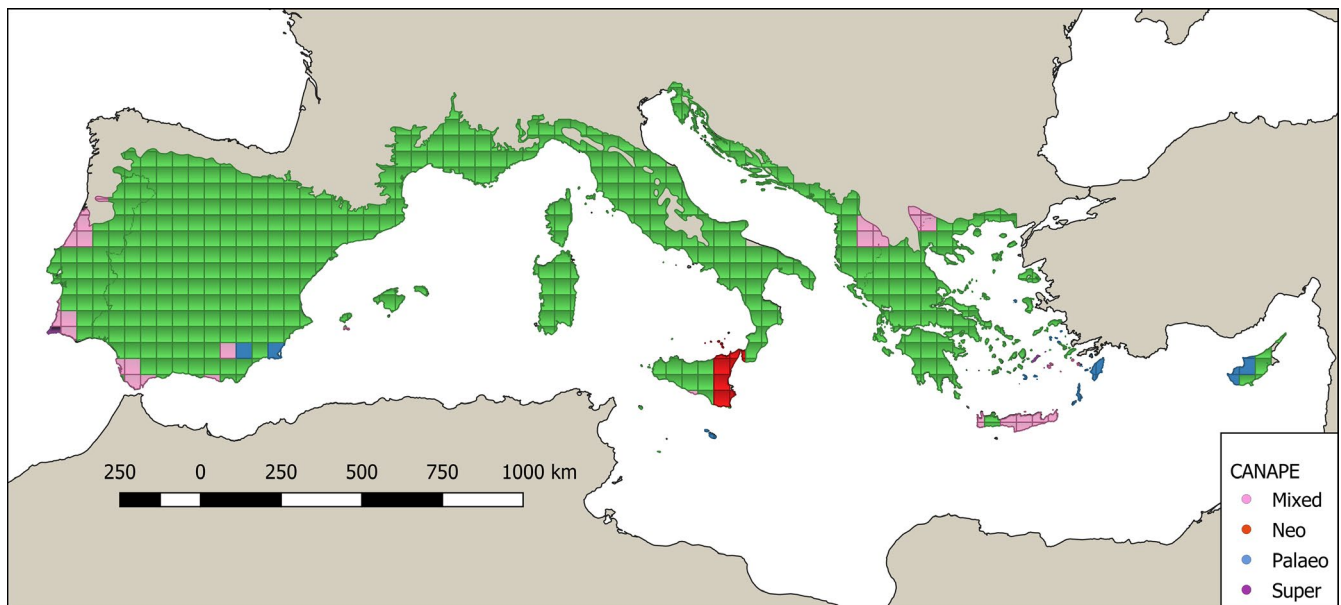


FIGURE 4 Map of the major centres of phylogenetic endemism in Mediterranean Europe. Green grid cells do not show any signal of phylogenetic endemism. Red grid cells contain significantly lower Relative Phylogenetic Endemism (RPE) than expected given random sampling of the same number of taxa from a null tree, termed “centers of neo-endemism.” Blue grid cells contain significantly higher RPE than expected, termed “centers of paleo-endemism.” Purple grid cells are a mixture of neo-endemism and paleo-endemism, the most highly significant of which (darker purple) are termed “centers of super-endemism.” Note that due to the scale of the map, not all significantly high phylogenetic endemism cells are visible

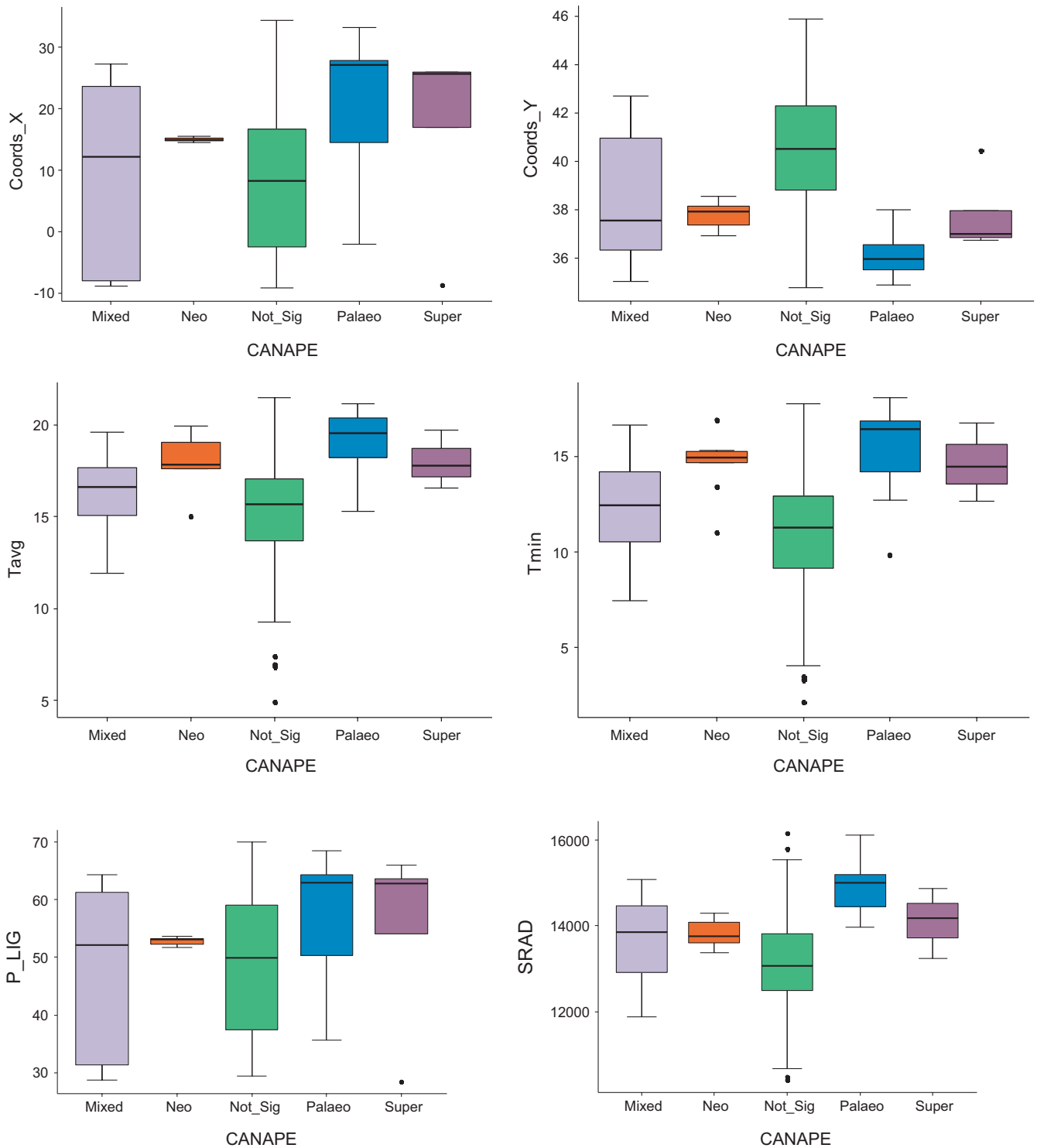


FIGURE 5 Boxplot of the distribution of the environmental variables depending on CANAPE category of each of the 643 cells analysed. The six environmental variables displayed (Coords_X, Coords_Y, Tavg, Tmin, LIG_prec and SRAD) are significantly different (Kruskal-Wallis test, $p < .05$) among CANAPE categories (see Table S3; $p < .05$; pairwise comparison using Wilcoxon test with HB correction). For each box, the bold horizontal line corresponds to the median; the lower and upper bounds of the box correspond to first and third quartiles, respectively; the upper vertical line extends from the upper bound of the box to the highest value of the distribution, no further than 1.59 interquartile range (IQR, or the distance between the first and third quartiles); the lower vertical line extends from the lower bound of the box to the lowest value of the distribution, no further than 1.59 IQR; black dots are values beyond IQR ("outlier" values)

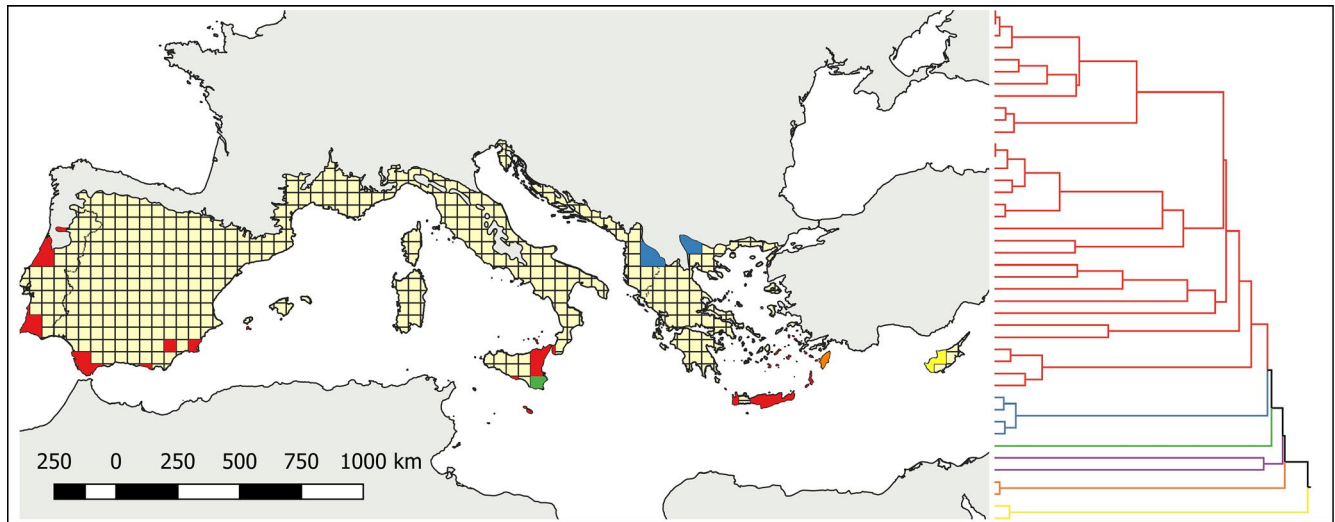


FIGURE 6 Range-weighted phylogenetic turnover among those cells found to be significant centres of endemism in CANAPE, showing that the greatest dissimilarity was observed between the coast of the southern and western Iberian Peninsula, north-eastern Sicily, and Crete and the rest of the Euro-Mediterranean region. These formed a grouped cluster whereas the rest of Mediterranean region formed a discrete cluster

and Last Glacial Maximum) climate variables, the high diversity east- and west-Mediterranean areas were correlated with soil and older (Last Inter-Glacial) climate variables. Soil water capacity, soil organic carbon stock, the coarse fragments and silt content proved important factors here although substrate type, soil nutrient content and soil structure are more regularly associated with phylogenetic diversity under different biogeographic settings (Alvarez et al., 2009; Haerdle et al., 2003; Jiang et al., 2015; Laliberté et al., 2013). Although rarely done, the Mediterranean, with its high diversity of soil types, could be a good model to further test and understand the importance of the comparatively lesser studied edaphic variables on plant differentiation (Kruckeberg, 2004).

Such spatial patterns are known in the Mediterranean and both north-south and west-east spatial biodiversity gradients have been described before (Conord et al., 2012; Médail & Diadema, 2009; Rodríguez-Sánchez & Arroyo, 2008). The fact that longer term and older environmental variables explain the east-west spatial structure of diversity possibly indicates a longer-lasting biodiversity structure than the one opposing southern and northern areas in Mediterranean Europe (Duggen et al., 2003; Krijgsman et al., 1999). Worldwide, latitudinal patterns in taxonomic turnover are ubiquitous and have long been known to reflect a universal latitudinal climate gradient (Darwin, 1859 – chapter 11). In this part of world, there is a strong longitudinal variation in floristic regions (Macaronesian, Mediterranean, Irano-Turanian) which is tightly related to the paleogeographic and paleoclimatic history of the Tethyan Basin (Takhtajan, 1986). Past geological events, ecological factors and evolutionary history may all have contributed to the longitudinal biodiversity pattern found here. Disentangling their importance would require a comparison with other regions where longitudinal patterns also exist, such as in Eurasia (Takhtajan, 1986).

Phylogenetic endemism was the least significantly correlated of all phylogenetic indices, thus adding a new dimension to the

taxonomic richness and phylogenetic diversity analysis of European Mediterranean tree genera. Latitude has a crucial influence on all components of alpha diversity (phylogenetic diversity, phylogenetic endemism and Rao phylogenetic diversity). Most diversity rich areas are found in southern coastal Spain, south-eastern Italy, southern Greece and southern Sardinia, which correlates well with current climate variables. These areas of high topographic variability are also areas of relative Pleistocene climate stability and low temperature change velocity, which are known to harbour high levels of species endemism (Jansson, 2003; Sandel et al., 2011; Tzedakis et al., 2002). However, phylogenetic endemism behaves somewhat differently and increases towards the east of the Mediterranean Basin, emphasizing again the importance of this region of relatively mild Mid-Holocene and LGM temperature and high Mid-Holocene annual precipitation, as shown in previous Mediterranean-wide studies (Conord et al., 2012; Médail & Diadema, 2009), helping the persistence of taxa with longer branch lengths.

4.2 | Identifying regions of high phylogenetic neo- and paleo-endemism

Endemic plants can be relicts or newly formed, and these two categories of endemic taxa are commonly referred to as paleo-endemics or neo-endemics, respectively (Favarger & Contandriopoulos, 1961; Stebbins & Major, 1965; Thompson, 2020). Hence, paleo-endemic taxa are ancient or relict elements of a given taxonomic group, often systematically isolated from other taxa, and neo-endemic taxa are more recently evolved and have extant sister taxa. Extending the notion of endemism to phylogenetic diversity in a spatial context, a high representation of phylogenetic paleo-endemism can be indicative of an area that has been a long-term refugium while phylogenetic neo-endemism, with an over-representation of short branches that are rare on the

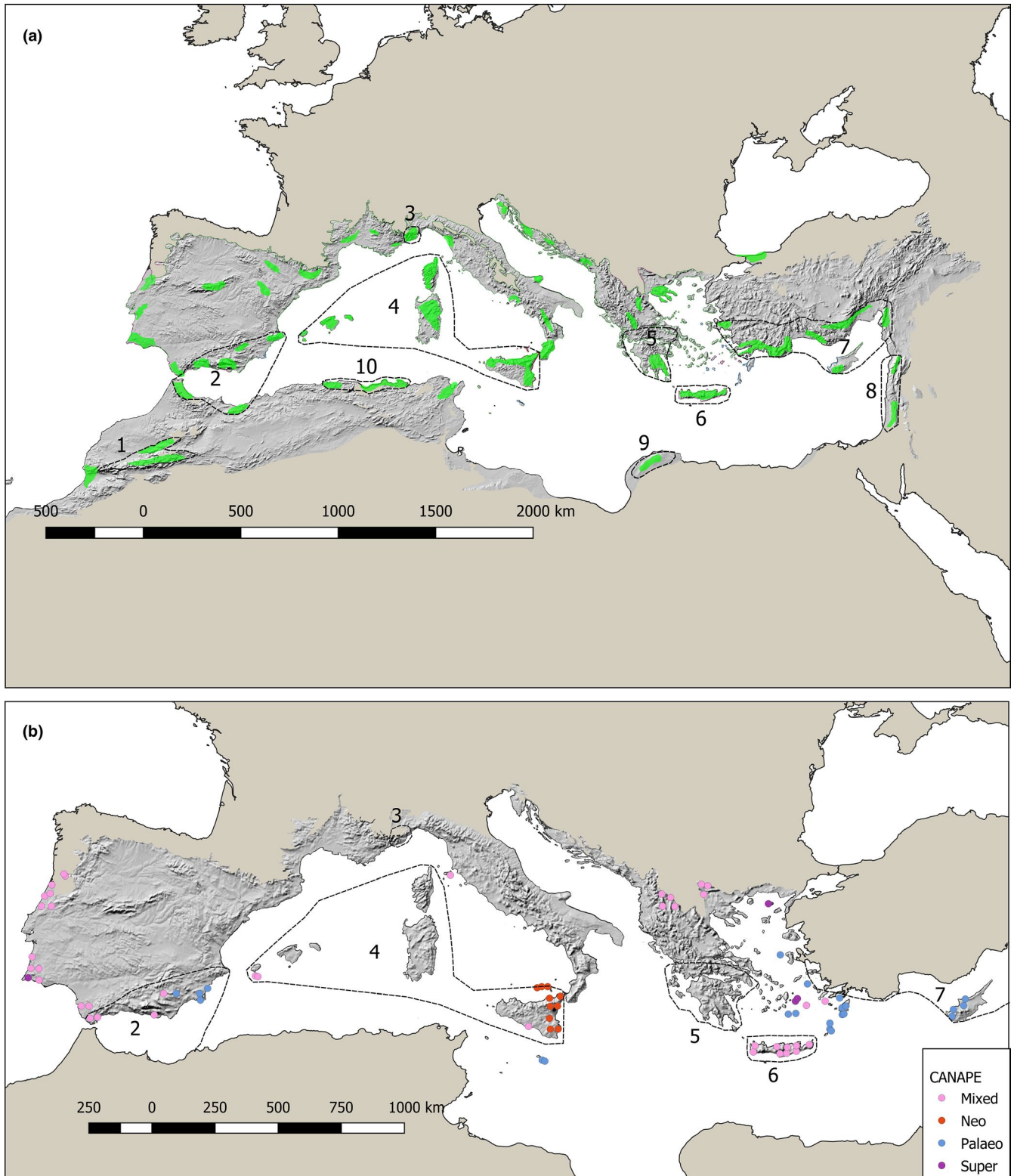


FIGURE 7 Map in shaded relief (Becker et al., 2009) of the biogeographical limits of the Euro-Mediterranean region following the scheme of Olson et al. (2001). (a) The location of the 52 putative refugia (green) identified by Médail and Diadema (2009) and of the 10 regional hotspots of plant biodiversity (large broken line) identified by Médail and Quézel (1997) and Vela and Benhouhou (2007). 1, High and Middle Atlas; 2, Baetic–Rifan complex; 3, Maritime and Ligurian Alps; 4, Tyrrhenian islands; 5, south and central Greece; 6, Crete; 7, south Anatolia and Cyprus; 8, Syria–Lebanon–Israel; 9, Mediterranean Cyrenaic; 10, Kabylies–Numidie–Kroumirie. (b) The location of the 76 centres of phylogenetic endemism at genus level identified in this study. Red dots indicate centres of neo-endemism, blue dots centres of paleo-endemism, purple dots centres of mixed-endemism (both neo and paleo-endemism) and dark purple dots centres of super-endemism. Dashed black lines represent the contours of the six regional hotspots of plant biodiversity that occur in Mediterranean Europe

landscape, can indicate a place of recent lineage divergence with close relatives occurring in the same communities (Mishler et al., 2014), possibly due to local conditions such as specific isolated substrates. As we deal here with tree genera, thus rather deep time phylogenetic events, areas of paleo and neo-endemism are likely to result from deep time historical events, earlier than the Tertiary (see phylogenetic tree of Cheikh Albassatneh et al., 2020). And, consequently, we may have missed more recent neo-endemism patterns such as ones that could have been detected if we had used species-level data, although tree genera are not particularly speciose in the Euro-Mediterranean region.

As mentioned by Mishler et al. (2020), when a lineage is widespread outside a study region, yet rare within it, CANAPE treats it as a range-restricted lineage in the region, increasing its contribution to the endemism analyses. This is possibly the case here at the southern and eastern edges of our study area where phylogenetic paleo- and neo-endemism is high, as they mark the transition with other floristic regions (Saharo-Arabian, Irano-Turanian) while still harbouring an important part of Mediterranean flora. Sampling trees only and using an ad hoc phylogeny may also result in biased phylogenetic endemism estimates (Park et al., 2018), although we consider this risk limited here as the time-calibrated phylogeny used fits well with the APGIV global plant phylogeny (Chase et al., 2016; Cheikh Albassatneh et al., 2020). Any spatial phylogenetic study that is not worldwide will display edge effects, no matter how well-done the sampling is. Here, we consider that high PE cells located at the edge of our study area have a high conservation value per se and should not be considered as artefacts because our endemism study is relative to our study area. Mediterranean Europe habitat managers will target these areas of local phylogenetic endemism as relevant high priority conservation value.

Based on the phylogeographic structure of plant species, Médail and Diadema (2009) identified 52 refugia within the Mediterranean region, 33 situated in the western Mediterranean Basin and 19 in the eastern part. Our study identified 76 grid cells of high phylogenetic endemism (22 paleo-endemism, 10 neo-endemism, 40 mixed-endemism, 4 super-endemism), 38 situated in the western and 38 in the eastern Mediterranean Basin, which mostly match regions considered as regional hotspots of plant biodiversity (Médail & Quézel, 1997; Vela & Benhouhou, 2007) and are refugia-rich in the study of Médail and Diadema (2009) (Figure 7).

In addition, eastern Sicily can also be identified as a hotspot of phylogenetic neo-endemism. South-western Andalusia, the Greek islands of Psara, Karpathos and Rhodos, and Cyprus also concentrate high phylogenetic paleo-endemism. The southern and eastern regions of the Iberian Peninsula and Crete are also rich for phylogenetic mixed-endemism. While Portugal and the southern tip of Spain are not a biodiversity hotspot, they are rich in refugia and phylogenetic mixed-endemism.

The high concentration of mixed phylogenetic endemism that we identified in northern Greece and the Belasica mountains of Bulgaria, and of super-endemism in a few Greek Aegean Islands (Samothraki, Amorgos) were neither detected as regional hotspots of plant biodiversity by Médail and Quézel (1997) or as refugia by Médail and

Diadema (2009). They can be added to the list of important plant biodiversity areas of the Mediterranean Basin. Overall, as indicated by the phylogenetic turnover analysis, the hotspots of phylogenetic endemism of the coast of the southern and western Iberian Peninsula, north-eastern Sicily and Crete, were more similar to each other than to those the Balkans and Cyprus.

Centres of paleo-endemism are associated with wet and equable climatic conditions similar to those of ancient pre-Mediterranean climates (Anacker & Harrison, 2012; Herrera, 1992; Jansson, 2003; Médail & Diadema, 2009; Raven & Axelrod, 1978). These types of humid refugia can be found at the mid-altitude (approximately 400 to 800 m altitude) and in sea level ravines such as for *Phoenix theophrasti* in Crete. In northern Greece, mesic ravine forest community types that are putative Pleistocene refugia, showed significantly high phylogenetic diversity compared with other forest community types (Mastrogianni et al., 2019). Such areas, less arid than the surrounding dry plains and less cold than higher elevation or latitude sites may have allowed rapid altitudinal shifts in response to climate change, in situ persistence of species and the emergence of endemism (Beug, 1975; Jansson, 2003; Sandel et al., 2011; Tzedakis et al., 2002). This is the case in many regions such as in the mountains of southern Spain (Arroyo & Marañón, 1990; Cañadas et al., 2014), Balearic Islands (Contandriopoulos & Cardona, 1984) and the Ioannina catchment in the Pindus Mountains of Greece. Our study confirms south-eastern Spain as an area of both paleo- and neo-endemism (such as the Natural Park Sierras de Cazorla, Segura and the Villas, Cabo Tiñoso and Roldán Sierra in the north-west of Murcia) and provides evidence of paleo-endemism in the islands of Cyprus, and of the Dodecanese and Cyclades in Greece, where such phylogenetically original genera as *Phoenix* and *Liquidambar* can be found.

Studies of the California flora concluded that neo-endemic centres were in regions with relatively young Mediterranean climate and high relative geomorphological heterogeneity (Lancaster & Kay, 2013; Raven & Axelrod, 1978; Stebbins & Major, 1965). From a phylogenetic point of view, neo-endemics result from recent in situ differentiation. Worldwide, closely related neo-endemics are usually found in the same area or in adjacent regions, often constituting groups of vicarious taxa (Cowling & Holmes, 1992; Kruckeberg, 2004). Thus, centres of neo-endemism are more related to harsher environmental conditions (Cacho & Strauss, 2014; Verdú & Pausas, 2013) and to high topographical relief encouraging spatial divergence (Crisp et al., 2001; Molina-Venegas et al., 2015, 2016; Vetaas & Grytnes, 2002). We identified only a few areas of phylogenetic neo-endemism in the Euro-Mediterranean region, located in the high topographical relief and high geological activity zones of eastern Sicily and southern Corsica.

5 | CONCLUSION

Low climate change velocity areas, with continuous warm-wet climates, contain high phylogenetic diversity and endemism in

the Mediterranean. Using phylogenetic endemism as an indicator, we confirm the high conservation value of: (a) the Aegean islands where several types of phylogenetic endemism were found, demonstrating long-lasting evolutionary processes, (b) eastern Sicily as a cradle of neo-endemism, (c) Cyprus as a museum of paleo-endemism, and (d) coastal southwest Portugal, the southern and eastern regions of the Iberian Peninsula, and Crete for mixed-endemism.

We demonstrate that trees of the Euro-Mediterranean region show clear patterns in the spatial distribution of their evolutionary heritage. We confirm that the southern large peninsulas and the islands of this region are regional hotspots of taxonomic richness, phylogenetic diversity and phylogenetic endemism. We identify several islands of the Dodecanese and Cyclades, the Belasica mountains in Bulgaria and northern Greece as areas of yet undetected high conservation value for their phylogenetic endemism. Future research should test whether protected areas actually fully encompass these phylogenetically rich areas.

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CONFLICT OF INTEREST

The authors have no competing interests to declare.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13241>.

DATA AVAILABILITY STATEMENT

All data are available open access, as indicated in the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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