

## RESEARCH ARTICLE

# Effect of environmental and spatial factors on the phylogenetic and functional diversity of the Mediterranean tree communities of Europe

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conservation; forest; functional trait; Mediterranean Basin; plastid DNA; phylogenetic analysis; phylogenetic signal of traits; tree.

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## ABSTRACT

- The tree flora of the Mediterranean Basin contains an outstanding taxonomic richness and a high proportion of endemic taxa. Contrary to other regions of the Mediterranean biome, a comprehensive phylogenetic analysis of the relationship between phylogenetic diversity, trait diversity and environmental factors in a spatial ecological context is lacking.
- We inferred the first calibrated phylogeny of 203 native tree species occurring in the European Mediterranean Basin based on 12 DNA regions. Using a set of four functional traits, we computed phylogenetic diversity for all 10,042 grid cells of 10 × 10 km spatial resolution to completely cover Mediterranean Europe. Then, we tested the spatial influence of environmental factors on tree diversity.
- Our results suggest that the nature of the relationship between traits and phylogeny varies among the different studied traits and according to the evolutionary distance considered. Phylogenetic diversity and functional diversity of European Mediterranean trees correlated strongly with species richness. High values of these diversity indices were located in the north of the study area, at high altitude, and minimum temperature of the coldest month. In contrast, the two phylogenetic indices that were not correlated with species richness (Mean Phylogenetic Distance, Phylogenetic Species Variability) were located in the south of the study area and were positively correlated with high altitude, soil organic carbon stock and sand soil texture.
- Our study provides support for the use of phylogenies in conservation biology to assess ecosystem functioning, and provides insights for the implementation of sustainable forest ecosystem management.

## INTRODUCTION

Biodiversity, the variety and variability among living organisms and the ecological complexes in which they occur, is a central concept in the life sciences; this includes diversity within species, between species, and of ecosystems (Gaston 1996). Biodiversity-ecosystem functioning research has shown that the functioning of a biological community is mediated by the diversity of its component species (Hooper *et al.* 2005; Cardinale *et al.* 2011). Most experiments reveal that ecosystem function has a positive relationship with species richness (Cardinale *et al.* 2011). However, biodiversity is not just species richness; in experimental data, species richness typically accounts for between 30–73% of the variance of a given ecosystem function (Cardinale *et al.* 2006). This wide range has prompted ecologists to look for measures of diversity that more reliably explain variation in ecosystem function, including estimates of phylogenetic and functional diversity (Reiss *et al.* 2009; Cadotte *et al.* 2011; Naeem *et al.* 2012).

Phylogenetic diversity is the full set of nested clades representing phylogenetic relationships among organisms at all levels. The perception of biodiversity patterns becomes more complete when phylogenetic methods are added to traditional species-based methods (Forest *et al.* 2007; Rodrigues *et al.* 2011). Phylogenetic relationships among species have been incorporated into diversity analyses since the 1990s (Faith 1992; Cadotte *et al.* 2009; Pavoine *et al.* 2010).

Measures of functional diversity are typically based on a subset of traits of the component species that are known to be important for ecosystem functions (Petchev *et al.* 2004). In general, such measures require careful *a priori* consideration of which traits to include, and whether or not traits should receive different weights. Despite these complications, functional diversity measures often better explain variation in ecosystem function than species richness and other taxonomic diversity measures (Petchev *et al.* 2004; Flynn *et al.* 2011). Functional diversity or trait diversity refers to the diversity of the value and range of species or organism traits (Díaz & Cabido 2001; Tilman 2001;

Ricotta 2005; Petchey & Gaston 2006, 2007; Swenson 2012; Swenson *et al.* 2012). Functional diversity is regarded as key to understanding ecosystem processes and their response to environmental change or disturbance (Norberg *et al.* 2001; Cornelissen *et al.* 2003; Suding *et al.* 2008; Cadotte *et al.* 2009; Flynn *et al.* 2011). In addition, functional traits represent an evolutionary response to climate, water relations, carbon gain and competition (Wright *et al.* 2004; Donovan *et al.* 2011). Consequently, functional traits are key to determining the interactions between plant species and their environment (Sattichanh *et al.* 2015). Large datasets of functional diversity measures have been developed in the literature (Walker *et al.* 1999; Petchey & Gaston 2002, 2006; Díaz *et al.* 2007; Villéger *et al.* 2008; Poos *et al.* 2009; Schmera *et al.* 2009; Laliberté & Legendre 2010; Mouchet *et al.* 2010; Chiu & Chao 2014).

Functional diversity and phylogenetic diversity are expected to be related, as functional traits are often characterized by polygenic inheritance (Kelly *et al.* 2014), which generally relies on the hypothesis that closely related species are more functionally similar than distantly related species, and therefore a more phylogenetically diverse community will have greater functional complementarity (Srivastava *et al.* 2012). However, the links between them are never that simple because of the possibility of convergence in traits between distantly related species or divergent selection between closely related species (Cianciaruso *et al.* 2012; Kelly *et al.* 2014).

Use of phylogenetic diversity (PD) indices as a proxy for functional diversity (FD) implies the existence of a relationship between the phylogeny and traits (Flynn *et al.* 2011; Srivastava *et al.* 2012; Swenson *et al.* 2012; Pavoine *et al.* 2013). This relationship has made the use of phylogenetic diversity very promising in biodiversity of ecosystem function science, because high-quality phylogenies with complete taxon sampling are now relatively easy to obtain (Joly *et al.* 2014). While good-quality trait data are costly and time-consuming to gather and still scarce and patchy at best, or even nonexistent for some species, ecosystems, or traits (Winter *et al.* 2013). Nevertheless, the relationship between phylogenetic and functional diversity is not that simple because trait evolution may not adjust the phylogenetic structure (trait homoplasy from convergence or reversion). Thus, the studies that investigated the phylogenetic signal contained in traits at a community level found divergent results: while there are studies that provide little phylogenetic information in traits studied in temperate and tropical tree communities (Swenson *et al.* 2012), investigation of plant grassland communities showed a much stronger influence of phylogeny on traits in one instance (Kembel & Cahill Jr 2011), but see Perronne *et al.* (2014).

The tree flora of the Mediterranean Basin is particularly remarkable and far more species-rich than that of temperate Europe (Quézel & Médail 2003). This region stands out due to its high topographic, edaphic and climatic heterogeneity that has allowed the evolution and long-term persistence of a diversity of conifer and angiosperm tree taxa, both sclerophyllous and deciduous (Quézel & Médail 2003; Aurelle *et al.* 2022). Their current distribution reflects the complex palaeogeography of the region (Thompson 2005). Surprisingly, comprehensive phylogenetic and functional trait datasets are scarce for Mediterranean tree species. The only available large-scale, dated phylogeny was produced very recently and was done at the genus level (Cheikh Albassatneh *et al.* 2021). And the first

species dataset of traits and occurrences has only recently been assembled (Monnet *et al.* 2021). Both concern the tree species of the European part of the Mediterranean Basin. Our study is the first that investigates how functional traits co-vary with the phylogeny at different phylogenetic distances in the European Mediterranean forest tree species community.

This study is organized around four main goals: (i) to provide the first calibrated phylogeny of the 203 tree species native to Mediterranean Europe; (ii) to elucidate the relationship between functional traits and phylogenetic patterns in order to provide stronger arguments for the use of PD as a proxy for FD; (iii) to understand the strength and nature of the correlation between the phylogeny and functional traits, at all phylogenetic levels of tree species that have a significant impact on the functioning of Mediterranean European forests; and (iv) to investigate how a range of likely structured environmental and spatial factors drive taxonomic, functional and phylogenetic diversity at distance scale.

## MATERIAL AND METHODS

### Selection of tree taxa

The woody vegetation of the Mediterranean is made up of diverse types of shrublands (maquis, garrigue, phrygana) and forests, where tree morphology varies widely with environmental 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 the checklist of 203 native tree species and their spatial distribution provided in Monnet *et al.* (2021). For distribution, we used a total of 10,042 grid cells of 10 × 10 km spatial resolution to completely cover the European Mediterranean Basin (Monnet *et al.* 2021).

### Phylogenetic inference

In this study, we wanted to infer a calibrated phylogenetic tree for 203 species, with a well-defined topology and adequate for the standard phylogeny of vascular plants. Since the phylogenetic tree of 203 Mediterranean species will not provide a complete topology of vascular plants (absence of several clades and several orders, such as Nymphaeales, Magnoliales, ferns, *etc.*), inferring the phylogenetic tree was carried out by completing the list of 203 species using additional taxa from the main clades and orders of gymnosperms, angiosperms and ferns to infer an extended tree that contains the main clades and orders (Appendix S1).

### Acquisition of DNA sequence data

We used data from 12 DNA regions commonly used for phylogenetic and taxonomic barcoding purposes: (i) plastid genes (*matK*, *rbcL*, *ndhF*, *atpB*, *psbB*, *rpl16*, *trnQ-rps16*), (ii) plastid intergenic spacers (*trnL-trnF*, *psbA-trnH*), (iii) mitochondrial genes (*atp1*, *matR*), and (iv) ribosomal DNA (Internal transcribed spacer – ITS). In a first step, we gathered all available sequence data for our target taxa from NCBI (<https://www.ncbi.nlm.nih.gov/nucleotide/>; accessed July 2020) and from the datasets of Monnet *et al.* (2021) using *matrixmaker* (Freyman & Thornhill 2016) (Appendix S2). The only species that did not have any sequence available was *Salix appendiculata* Vill. and

was thus absent in our DNA sampling. According to data availability, we finally obtain sequences for 277 species.

#### Sequence alignment

For each DNA region separately, multiple sequence alignments were built using *MAFFT* (Katoh *et al.* 2002) and parsed using *Gblocks* (Castresana 2000) to exclude the segments characterized by several variable positions or gaps from the final alignment. A phylogenetic tree was inferred for each gene to detect abnormal species location in the single DNA region trees.

#### Supermatrix data assembly

We used a supermatrix approach (McMahon & Sanderson 2006; Sanderson *et al.* 2007) to combine our large datasets. We concatenated the DNA region clusters into a combined matrix, making sure there was species overlap between each cluster and at least one other cluster. In total, the supermatrix has 277 species and 11,722 sites (Appendix S3). This step was performed using the *Biopython* package (Cock *et al.* 2009) implemented in python (Van Rossum & Drake 2009).

#### Phylogenetic analysis

Phylogenetic analyses using maximum likelihood (Felsenstein 1973) were conducted using the Randomized Accelerated Maximum Likelihood program (RAxML version 8; Stamatakis 2014). We conducted analyses on all individual genes using the supermatrix dataset.

An appropriate substitution model of sequence evolution was selected for each of the 12 DNA regions using the Akaike Information Criterion (AIC) as implemented in the JModeltest 2 program (Darriba *et al.* 2012). The optimal substitution model identified was for all 12 DNA regions sequences: GTR + G. The GTRGAMMA nucleotide substitution model was used for all partitions, with the default settings for the optimization of individual per-site substitution rates. We applied the constraint tree option with a backbone tree using edge null tree of 277 species from *V. phyloMaker*, scenario 3 (Jin & Qian 2019) (Appendix S4 and S5).

We added the missing species, *Salix appendiculata*, to the tree of 277 species by applying the Simulation with Uncertainty for Phylogenetic Investigating (SUNPLIN) implemented in R, using the branch-based method as random insertion (Martins *et al.* 2013) (Appendix S6 and S7).

We estimated a chronogram of 278 species using the software *treePL* (Smith & O'Meara 2012) with 42 calibration points from the literature (Magallón *et al.* 2013; Rothfels *et al.* 2015) (Appendix S8 and S9).

Finally, we dropped the supplementary species from the extended tree of 278 species using the package *ape* (Paradis *et al.* 2004) implemented in R (R Core Team 2020) (Appendix S10) to limit the phylogenetic tree to the 203 European Mediterranean tree species.

#### Functional traits selection

We assembled a dataset of functional traits for the 203 tree species of the European Mediterranean region (Monnet *et al.* 2021) and calculated the mean value for each species. Only continuous traits were used that have demonstrated links to forest productivity. These were: (i) stem specific density (Swenson & Enquist 2007; Chave *et al.* 2009); (ii) seed dry mass (Ben-Hur

*et al.* 2012) – small-seeded species produce more seeds and the probability that one seed might reach a suitable new site is higher, consequently increasing naturalization success (Hamilton *et al.* 2005), while large seeds might also help in establishment because they have more storage tissue, which allows the seedling to be independent from external resources for a period of time (Jensen & Gutkunst 2003); (iii) specific leaf area (SLA) – species with higher SLA take up nitrogen easily and have a high relative growth rate (Hamilton *et al.* 2005), SLA also represents light-capturing area deployed per dry mass allocated, and is closely correlated with other plant traits, such as photosynthetic capacity, leaf N content, leaf life-span and, importantly, relative growth rate (Reich *et al.* 1997); and (iv) plant maximum height, which is correlated with competitive ability, improving naturalization success (Bucharova & Van Kleunen 2009), and relates positively to native distribution size (Lavergne *et al.* 2004; Petchey & Gaston 2006; Mokany *et al.* 2008; Bucharova & Van Kleunen 2009; Mace *et al.* 2010; Paquette & Messier 2011).

#### Topological difference metrics

A functional tree was then inferred using hierarchical clustering calculated from Euclidean distance and UPGMA on the functional traits (Legendre & Legendre 2012) using the R *vegan* package (Oksanen *et al.* 2022). We performed a Mantel test to compare distance matrices (Mantel 1967), with pairwise Abouheif's distance for the phylogenetic tree and Euclidean distances for the traits (Abouheif 1999; Pavoine *et al.* 2008; Hardy & Pavoine 2012) using the R *adephylo* package (Jombart *et al.* 2010) and R *vegan* package (Oksanen *et al.* 2022). After which the phylogenetic and functional trees were compared using the topological difference metric from Penny & Hendy (1985). The relative topological difference (RTD) was calculated as the proportion of the topological difference between the two trees, as:

$$\text{RTD} = \frac{\text{Topological difference}}{2n-6}$$

Ranging from 0 (no difference) to 1 (completely different), where  $n$  is the number of species and  $2n-6$  is the maximum number of topological differences. Trees were also compared using the branch length score (BLS) from Kuhner & Felsenstein (1994) in *ape* (Paradis *et al.* 2004), which takes branch length into account in addition to the number of branches that differ between trees (Steel & Penny 1993). The trees were always considered as unrooted.

#### Phylogenetic signals

The phylogenetic signal of traits is the tendency of related species to resemble each other for that trait more than species drawn at random from the same tree (Münkemüller *et al.* 2012). Concerning the trait data (continuous characters), the phylogenetic signal of each trait was estimated using Pagel (1999); essentially,  $\lambda$  is the transformation of the phylogeny that ensures the best fit of trait data to a Brownian motion model. Therefore, when  $\lambda = 1$ , the structure of the phylogeny alone can explain changes in traits. In this case, traits follow a pure Brownian motion model of evolution. Alternatively, when  $\lambda = 0$ , the phylogeny has to become a 'star phylogeny' (*i.e.* lose



all its structure) to be able to explain trait evolution under a Brownian motion model. Therefore, the phylogeny alone does not explain trait evolution. In addition,  $\lambda$  can be  $>1$ , which would suggest that the rate of evolution of a trait is higher at the root than it is at the tip (Pagel 1999; Freckleton *et al.* 2002). The  $P$ -value likelihood ratio was estimated using the likelihood ratio test (LRT). This method compares the likelihood of an evolutionary model with the observed  $\lambda$  against that of a model where  $\lambda$  is fixed to zero. These analyses were performed in R using the *Geiger* package (Harmon *et al.* 2008), function *fitContinuous*.

After calculating  $\lambda$ , the nature of the autocorrelation of traits at different phylogenetic scales (distances) was investigated using  $I$ , Moran's autocorrelation coefficient (Moran 1950; Gittleman & Kot 1990). Moran's  $I$  is usually known as a measure of spatial autocorrelation in landscape ecology used to describe the spatial structure of a trait. However, in a phylogenetic context, it uses the phylogenetic proximity among species, instead of spatial proximity. This is essentially the same idea as using correlograms in landscape ecology (Legendre & Legendre 2012). The method divides the tree into slices of different distances and evaluates Moran's  $I$  only for the species grouping within a given slice at a one time. First, it compares the species that have diverged very recently, then species that have diverged for a slightly longer time, and so on. This allows checking if species are more or less similar than expected at a given distance class (Paquette *et al.* 2015). However, the use of this form of correlogram could be potentially limited for small trees and when tips are not uniformly distributed within the phylogeny. To avoid this potential problem, we used the *phylosignal* package, which is able to reconstruct the phylogenetic correlogram for which the autocorrelation can be computed continuously (Keck *et al.* 2016). Moran's  $I$  can be seen as an autocorrelation coefficient describing the relation of cross-taxonomic trait variation to phylogeny. Moran's  $I$  has a value between  $-1$  and  $+1$ . A positive Moran's  $I$  value at a given diversification time indicates that species of that diversification time tend to have more similar traits than when all species are considered, while a negative value suggest the opposite (Moran 1950; Gittleman & Kot 1990; Hackathon *et al.* 2011; Keck *et al.* 2016). Moran's  $I$  and phylogenetic autocorrelograms make the implicit assumptions that traits evolve similarly across the phylogeny. However, Keck *et al.* (2016) showed that this is rarely the case and that phylogenetic signal is scale-dependent and varies among clades. To test this dependency, Keck *et al.* (2016) proposed the Local Indicators of Phylogenetic Association (LIPA) index. This index computes local Moran's  $I$  for each tip of a tree to detect hotspots of positive and negative autocorrelation.

Comparative analyses were performed in R (Core Team 2020) using the *ape* (Paradis *et al.* 2004) and *phytools* packages (Revell 2012). We used *phylobase* (Hackathon *et al.* 2011), *ade-phylo* (Jombart *et al.* 2010), and *gtools* packages (Warnes *et al.* 2015) to plot the results.

#### Functional and phylogenetic alpha diversity and environmental factors

Using the calibrated phylogenetic tree and the matrix of species occurrence ( $10 \times 10$  km), we computed phylogenetic diversity metrics that were mathematically independent of species richness (SR). The phylogenetic diversity index corresponds to the sum of the branch lengths of a phylogenetic tree connecting all species in a community (PD; Faith 1992). The phylogenetic

species variability index (PSV; Helmus *et al.* 2007; Winter *et al.* 2013) is based on species presence/absence and their phylogenetic relationships. For a sample of  $n$  species,

$$PSV = \frac{ntrC - \sum C}{n(n-1)},$$

where  $C$  is the  $n \times n$  sample phylogenetic covariance matrix,  $trC$  is the sum of diagonal elements of  $C$ , and  $\sum C$  is the sum of all elements of  $C$ . As species in a sample become more closely related, PSV decreases toward zero; on the other hand, as species become less closely related, PSV increases toward 1. The extreme value of  $PSV = 1$  occurs if all species in the community are completely unrelated to each other. We can see that the statistical expectation of PSV is independent of species richness, thus any change in PSV due to disturbance is not a statistical artefact of varying species richness (Helmus *et al.* 2007).

We also calculated MPD (mean phylogenetic distance) between each sampled taxon and every other tip in the phylogeny, (it is used as a tool for deciding if the species of a given group or communities are closely related), and MNTD (mean nearest taxon distance: mean distance between each sampled taxon and its own most closely related taxon in the phylogeny) indices (Webb *et al.* 2002).

Functional diversity was measured using the FD index (Petchey & Gaston 2006, 2007), which is defined as the total branch lengths of a functional dendrogram in which there are as many branch tips as species. We computed the dendrogram for all 203 species, and calculated FD from the total branch lengths connecting the subset of species present at a given grid. To produce the functional dendrogram, we used a combination of the extended Gower distance measure (Gower 1971; Legendre & Legendre 1998; Podani 1999) and an unweighted pair-group arithmetic average (UPGMA) clustering (Petchey & Gaston 2006, 2007). Then, to make FD unaffected by species richness, we computed the Functional dispersion (FD<sub>dis</sub>) index, which corresponds to the mean distance of individual species to the centroid of all species in the multidimensional trait space (Laliberté & Legendre 2010),

#### Observed and expected functional diversity within habitats

To test whether the observed congruence between phylogenetic and functional diversity reflected ecological processes or were simply due to sampling effects, and to assess whether habitats exhibited a higher or lower level of phylogenetic or functional diversity than expected by chance, we calculated the standardized effect size (Gotelli & McCabe 2002; Manly & Sander-son 2002). The standardized effect size is calculated by standardizing the difference between the observed index ( $I_{obs}$ ) to the mean of the 999 indices from the simulated communities (null distribution) ( $I_{sim}$ ), which is "the pattern expected in the absence of species interactions" divided by the standard deviation of the 999 indices from the simulated communities ( $\sigma_{sim}$ ). The standardized effect size (SES) were estimated as:

$$SES = \frac{(I_{obs} - I_{sim})}{\sigma_{sim}}.$$

Negative values indicate phylogenetic or functional clustering, and positive values indicate phylogenetic or functional

overdispersion, with a significance threshold ( $\alpha = 0.05$ , two-sided) at  $-1.96$  and  $+1.96$ , respectively.

All alpha diversity indices and SES computations were carried out within the R environment (R Core Team 2020) using the *FD* and *picante* libraries (Kembel *et al.* 2010; Laliberté *et al.* 2014).

#### Environmental and spatial factors explaining alpha biodiversity indices

We computed the alpha diversity indices (Richness, FD, FDis, PD and PSVs), community phylogenetic indices (MPD and MNTD) and standardized for species richness effects. This standardization was used to remove implicit interdependence between species richness and phylogenetic diversity (SES.PD, SES.MPD and SES.MNTD). For each grid cell at a resolution of  $10 \times 10$  km, we modelled each diversity index as the response variable of predictor variables: (i) Climate variables from WorldClim, resolution 1 km (Fick & Hijmans 2017) (<http://www.worldclim.org/>): “Total annual precipitation” (Bio12, in mm), which approximates average water availability; “Precipitation of the driest month” (Bio14, in mm), which describes the extremes associated with drought events and stress due to low water availability; “Temperature seasonality” (Bio4, in T standard deviation  $\times 100$ ), which describes the variability of temperature during the year; and “Minimum temperature of the coldest month” (Bio06, in  $^{\circ}\text{C}$ ), which quantifies potentially lethal frost events and more generally, stress due to low temperatures. (ii) Soil variables from SoilGrids 250 m, resolution 250 m, from (Hengl *et al.* 2017; Shangquan *et al.* 2017) (<http://soilgrids.org/>): “Texture class” (USDA system) at a depth 0.30 m, “Soil organic carbon stock” in tons per ha for depth interval 0.00–0.30 m. Soil variables from <https://zenodo.org/record/4139912#.YOHzeej7S00> (Hájek *et al.* 2021) at a resolution 250 m: pH in water,  $\text{Ca}^+$  in water. We extracted the data for each cell using the R package *raster* (Hijmans *et al.* 2016), adjusted it to resolution  $10 \times 10$  km, then calculated the mean value of all raster pixels contained in the each cell. All description and acronyms of variables are provided in Appendix S11. All variables were standardized (mean = 0 and SD = 1) to make the regression coefficients comparable.

Relationships between diversity indices and associated variables were then estimated using ordinary least squares (OLS) models. To model spatial effects as well as incorporate predictors into the analysis, we used the spatial autoregressive error model (SARerr) (Kissling & Carl 2008).

We constructed the SARerr model using the package *spdep* (Bivand *et al.* 2006) implemented (R Core Team 2020) R version 4.0.3 for all analysis. We specified the neighbourhood distance based on the coordinates (longitude and latitude) of 10042 centroid grids and specified a maximum distance of 50 km, as outlined in Kissling & Carl (2008) using the function *dnearneigh*. Then, using the function *nb2listw*, we calculated the spatial weight matrix by weighting the neighbours with coding of the variance-stabilizing coding scheme (S) (Tiefelsdorf *et al.* 1999), and used maximum neighbour distance 50 km (Kissling & Carl 2008). The neighbourhood weighted was then defined as  $1/x$  where  $x$  equals 50 km. Finally, the SARerr model was specified by the function *errorsarlm*. As recommended in Kissling & Carl (2008), to minimize the Akaike information criterion (AIC), the environmental predictors were then added to this spatial model using a forward selection

strategy. All descriptor variables were examined for multicollinearity using the function *vif* in the package *car* (Fox & Weisberg 2019). To illustrate the relationship between all SARerr coefficients of alpha diversity indices, we prepared a table with diversity indices as rows and environmental variables as columns. We then standardized SARerr coefficients using Z-scores across the rows (indices) and computed a Principal Components Analysis (PCA) using the package *FactoMineR* (Lê *et al.* 2008) implemented in R. All R functions were run using R version (R Core Team 2020).

## RESULTS

There was ample variation and spatial patterns in all four traits examined across tree species in Mediterranean Europe (Fig. 1).

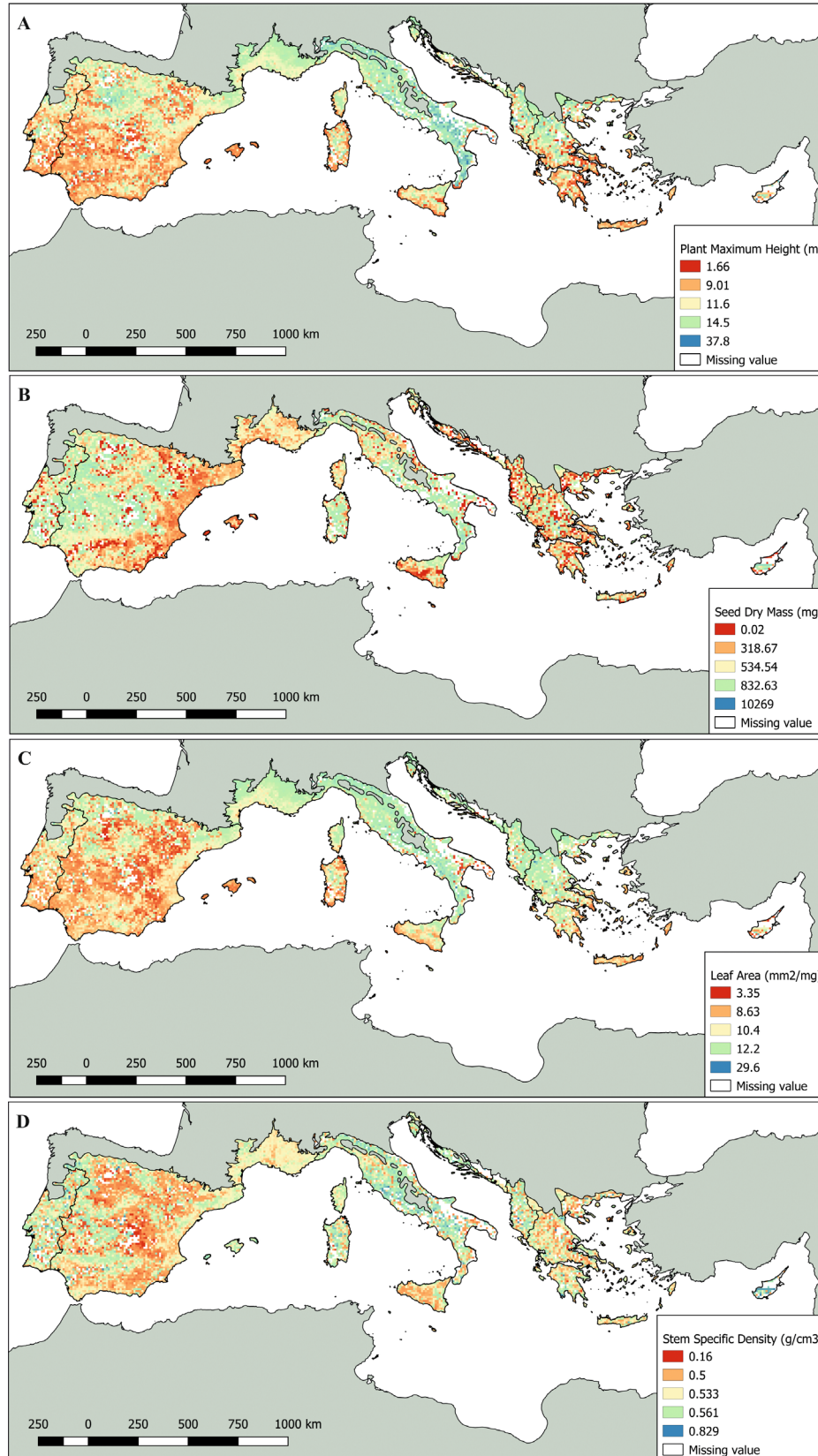
### Mismatch between phylogeny and function

The Mantel test revealed a weak, significant relationship between the distance matrices of phylogeny and functional distances ( $r = 0.11$ ,  $P < 0.05$ ), meaning that the phylogenetic and functional pairwise distances between the 203 Mediterranean trees species were correlated. The tree topologies based on the distance matrices for the phylogenetic and the trait data showed strong differences (RTD = 0.964; BLS = 4720.87; Appendix S12).

### Phylogenetic signal of traits

Page’s  $\lambda$  showed that species functional traits are linked to the evolutionary history of the species (Table 1, Appendix S13). Functionally similar species tend to be closely related, as is the case, for example, of the small-seeded *Betulaceae* and *Ulmaceae* and the large-seeded *Aesculus hippocastanum*, *Juglans regia* and *Quercus* species (Fagaceae). Additionally, stem specific density tended to be phylogenetically conserved, as is the case of all *Salicaceae* (*Salix*), *Sambucus*, and *Lonicera*, species that have a low density. Conversely, stem specific density was high in such related genera as *Buxus*, *Pistacia*, *Ostrya*, *Carpinus*, *Sorbus*, *Olea* and *Erica*. Concerning specific leaf area (SLA), the species were divided into two main groups. The first group was the gymnosperms, and genera *Spartium*, *Genista*, *Cytisus* from Fabaceae and from Ericaceae, which have a low SLA. The second group with a high SLA included the majority of the angiosperms, especially *Corylus*, *Ostrya* and *Fagus* (Appendix S13). Maximum plant height was clustered in the Pinaceae as well as in *Fagus* and some *Quercus* (*Q. canariensis*, *Q. petraea*, *Q. fraineti*) from the Fagaceae, and genera *Aesculus*, *Fraxinus*, *Ulmus*, *Acer*, *Tilia* and *Populus* from other plant families (Appendix S13). Whereas stem specific density had a comparatively lower Page’s  $\lambda$ , suggesting less dependence on the phylogeny, and all traits were found to display a high and significant phylogenetic signal (Table 1).

All traits had a significant positive Moran’s I at the most recent time scale, suggesting that trait values tend to be conserved in closely related species (tip of the phylogeny) (Fig. 2). However, at ancient time scale, all traits showed significant negative correlations, as illustrated in the diversification time (Fig. 2). For instance, seed dry mass and stem specific density showed significant positive correlations for the most recent times (Fig. 2), and this correlation decreased sharply for



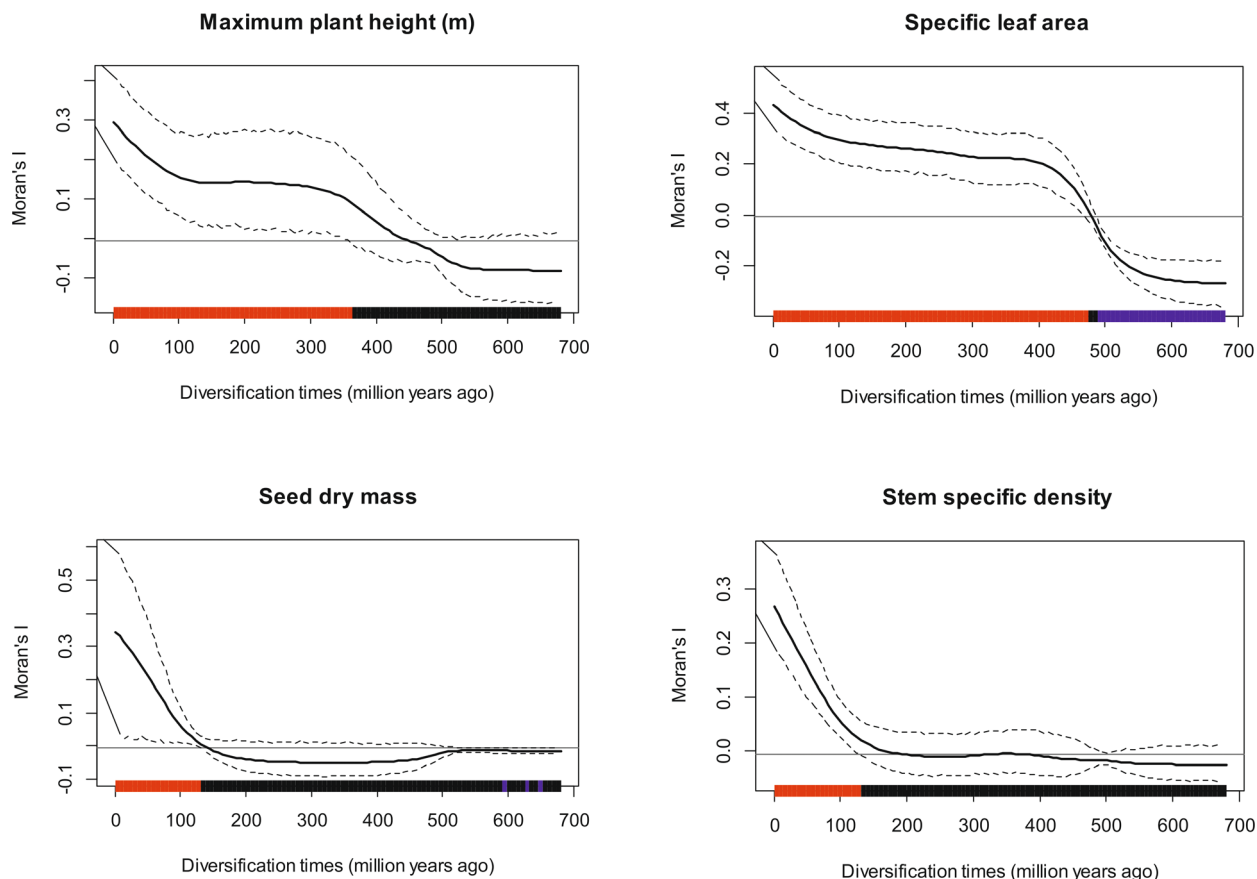
**Fig. 1.** Spatial distribution of trait values in Mediterranean Europe (five level scale). A: Plant maximum height, B: Seed dry mass, C: Specific leaf area, D: Stem specific density. Area outside of Mediterranean Europe is coloured light grey.



**Table 1.** Phylogenetic information in functional traits.

Functional trait	Unit	Trait code	Pagel's $\lambda$	Ln lik	Ln lik ( $\lambda = 0$ )	P value	delta.AICc
Plant maximum height	m	Height	0.89681801	-684.4811	-728.5308	<0.001	86.04
Seed dry mass	mg	SeedMass	0.99280659	-1600.2879	-1704.0228	<0.001	205.41
Leaf area per leaf dry mass	mm <sup>2</sup> ·mg <sup>-1</sup>	SLA	0.94177967	-520.5775	-602.3925	<0.001	161.57
Stem specific density	g·cm <sup>-3</sup>	StemSpecDens	0.78254468	163.5066	135.2829	<0.001	54.39

When values of Pagel's  $\lambda$  are close to 1 and significantly different from 0, the structure of the phylogeny alone can explain a high proportion of changes in traits. The *P*-value likelihood ratio was calculated using the likelihood ratio test (LRT) and indicates that Pagel's  $\lambda$  is significantly different from 0, indicating that the four functional traits evaluated are linked to the evolutionary history of species.



**Fig. 2.** Phylogenetic correlogram of four functional traits (maximum plant height, specific leaf area, seed dry mass and stem specific density) for 198 Euro-Mediterranean trees (excluding five species with missing trait data). The phylogenetic signal increased rapidly toward the tips in seed dry mass and stem specific density. However, the phylogenetic signal increased progressively toward the tips in maximum plant height and specific leaf area. The figure shows the mean phylogenetic signal (solid bold black line represents Moran's *I* index of autocorrelation) with a 95% confidence interval resulting from 100 bootstraps (dashed black lines represent both lower and upper bounds of confidence interval). The coloured horizontal bars show whether the autocorrelation is significant: red is a significantly positive autocorrelation, blue is a significantly negative autocorrelation, and black is a non-significant autocorrelation.

ancient times (100 Mya). On the other hand, SLA and maximum plant height showed significant positive correlations at recent times and these correlations started to decrease progressively over time (Fig. 2), suggesting a strong difference between gymnosperms and angiosperms for these two traits.

### Results of local indicators of phylogenetic association (LIPA)

The LIPA analyses revealed significant local positive autocorrelation for maximum plant height (Appendix S14, right panel, red dots) in the Pinaceae clade, and all nodes of the

Caryophyllales (Tamaricaceae), with the exception of *T. parvifolia*, clades of Eriaceae, clades of *Tilia* (Malvaceae), *Fagus* (Fagaceae), several clades of Salicaceae, several clades of Fagales (*Fagus*, *Castanea*, *Q. canariensis*, *Q. frainetto*, *Q. petraea*) and several clades of Rosales (*Ulmus*, *Crataegus pycnoloba*). Concerning seed dry mass, LIPA analyses showed local positive autocorrelation expanded in principal clades of Fagales (Fagaceae, *Corylus*, *Myrica* and *Juglans*) and clades of the genera *Myrica* and *Juglans* (Appendix S14, right panel, red dots). LIPA analyses revealed significant local positive autocorrelation for stem density (Appendix S14, right panel, red dots) in some

species of conifer in the Cupressaceae (*Juniperus oxycedrus* and *J. macrocarpa*) and Dipsacales in Adoxaceae (*Sambucus*), is several clades of Oleaceae and Sapindales, and whole clades of the Malpighiales (Salicaceae). Some clades of Fagales, especially *Carpinus* in Betulaceae, and some species of *Quercus* genus and *Sorbus* in Rosaceae (Appendix S14, right panel, red dots). Concerning SLA, LIPA analyses showed local positive autocorrelation in all clades of conifers, *Buxus*, and several clades of Fagales, especially Betulaceae, Juglandaceae and Myricaceae and *Fagus* in the Rosales and Ulmaceae in *Celtis* (Appendix S14, right panel, red dots).

### Relationship between phylogenetic and functional diversity

The results showed a significant relationship between PD and FD, whereas the relationship between the phylogenetic species variability (PSVs) and the functional dispersion was very weak ( $r=0.03$ ) (Fig. 3).

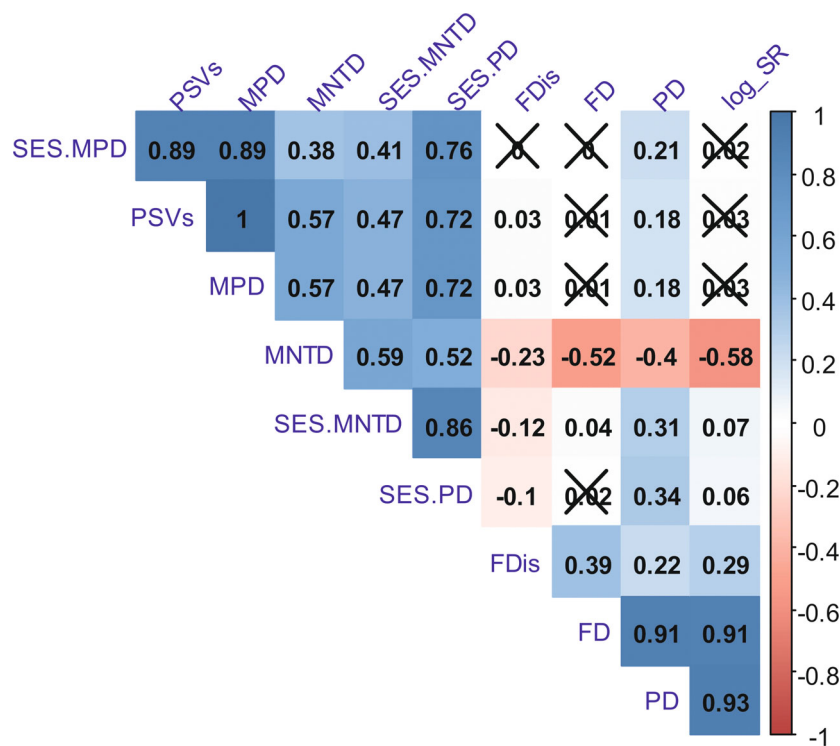
Species richness ( $\log_{10} SR$ ) was strongly correlated with PD ( $r=0.93$ ), FD ( $r=0.91$ ) and subsequently with MNTD ( $r=-0.58$ ). A much weaker correlation was observed between species richness and FDis ( $r=0.29$ ) (Fig. 3). Both MPD and MNTD were correlated with their standardized equivalents (MPD and SES.MPD:  $r=0.89$ ; MNTD and SES.MNTD:  $r=0.59$ ; see Fig. 3). Although neither showed a relationship with richness (PSVs, MPD:  $r=0.03$ ; Fig. 3). In Fig. 3, we found a strong correlation between MPD and PSVs ( $r=1$ ) (Appendix S15).

Across the whole of the grids cells, the mean of the standardized pairwise distance index (SES-MPD) and of the standardized mean nearest taxon distance index (SES.MNTD) were

both significantly below zero: SES.MPD mean =  $-0.064$ ,  $t$  test  $t=-5.477$ ,  $P<0.001$ ; SES.MNTD mean =  $-0.267$ ,  $t=-22.248$ ,  $P<0.001$ , indicating a general tendency of species phylogenetic clustering within communities. Moreover, we found SES.MNTD values were significantly lower than SES-MPD (Fig. 3, paired  $t$  test  $t=-15.675$ ,  $P<0.001$ ), indicating that species clustering was possibly more important near the tips of the tree.

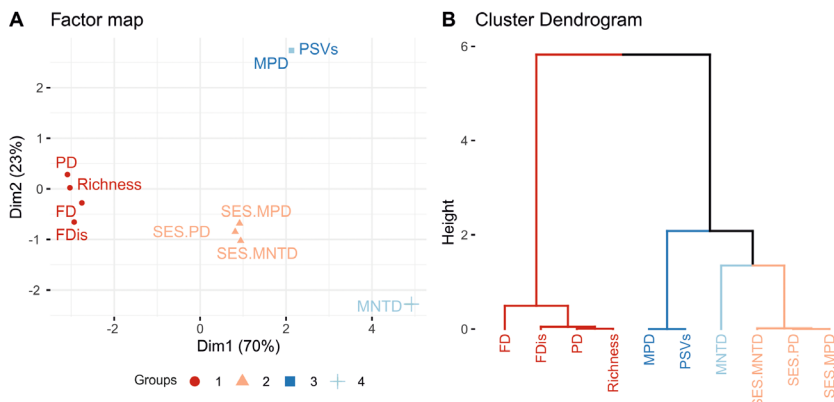
### Factors shaping phylogenetic and functional diversity

The results of the spatial autoregressive error model and the cluster analysis of PCA (Figs 4 and 5) showed a positive association between PD, FD, FDis and richness and the variables latitude “South–North gradient” and minimum temperature of the coldest month. PD was strongly correlated with the latitude “South–North gradient” and minimum temperature of the coldest month. High values of PD were concentrated in southern North Macedonia, Mediterranean France, the north Spanish coast, Corsica, northwest Italy (Province of Toscana), southeast Slovenia and southern Croatia (Appendix S18). High values of species richness were concentrated in southeast and southwest North Macedonia, Mediterranean France and northern Spain (Appendix S18; Fig. 6). Our results showed a positive association between MPD and PSVs (Figs 4 and 5) and low latitude “South”, high altitude, texture class, and soil organic carbon stock (OMS) (Figs 4 and 5). This pattern was concentrated in western and central Spain, and located sparsely in Cyprus, Greece and Italy (Appendix S18; Fig. 6). On the other hand, MNTD was negatively associated with altitude, latitude and minimum temperature of the coldest

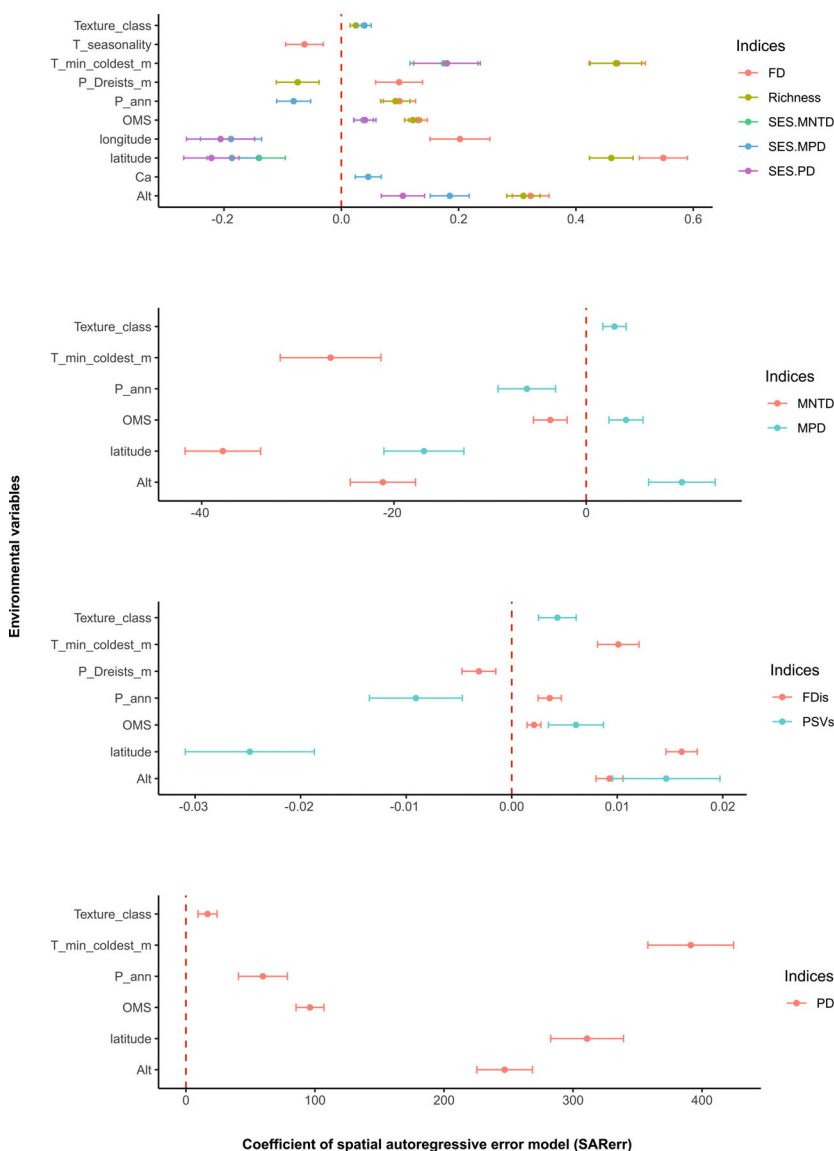


**Fig. 3.** The correlogram shows Pearson correlation coefficients for all pairs of variables (with more intense colours for more extreme correlations), and correlations not significantly different from 0 at  $P=0.01$  are represented by a white and cross box.

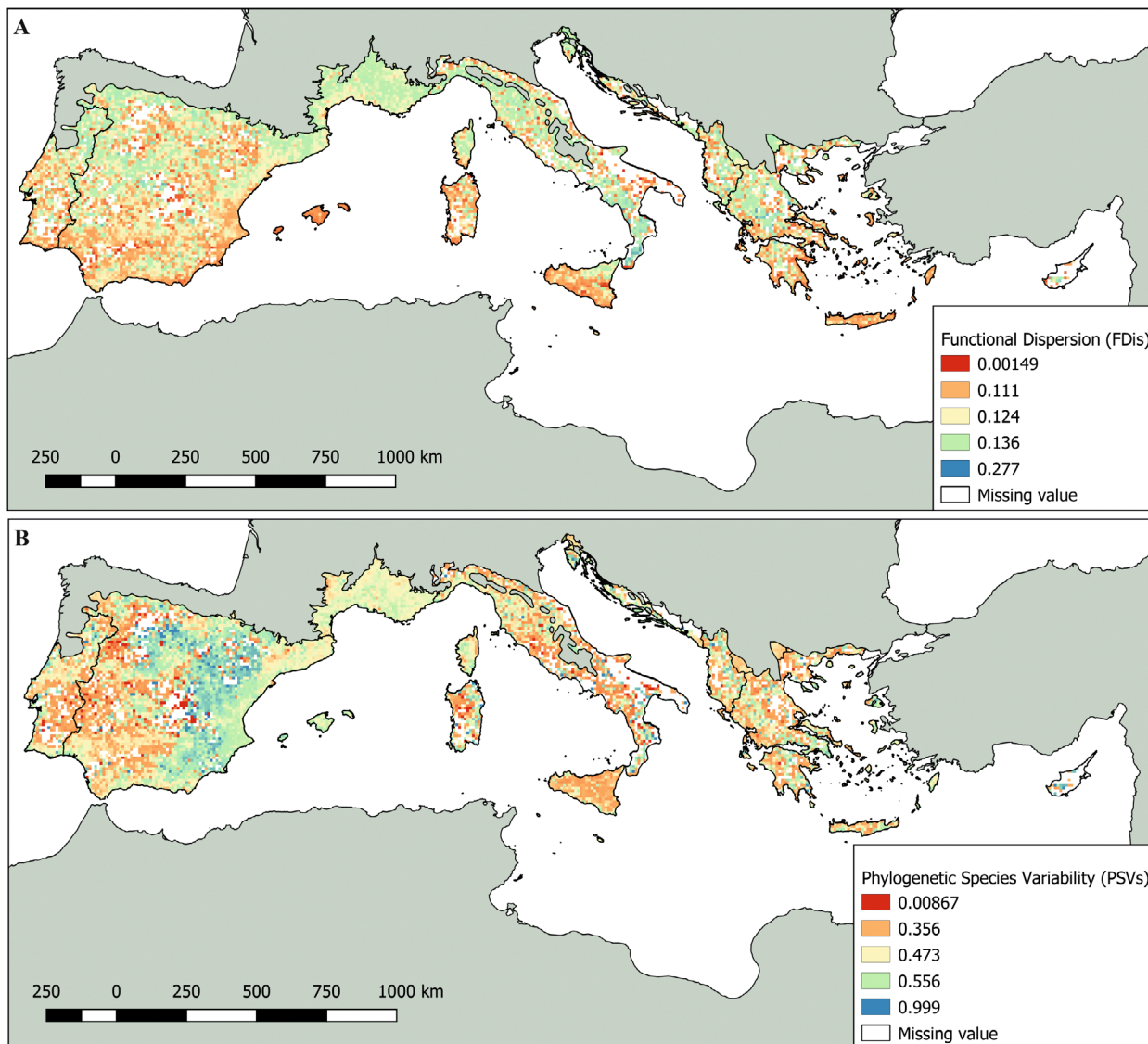




**Fig. 4.** Principal components analysis (A: factor map; B: cluster dendrogram) of the standardized coefficient of SARerr result, based on Z-score standardization of row of the SARerr coefficients table, showing: (1) clustering of PD, FD, FDis and Richness, (2) clustering of MPD, PSVs, (3) MNTD, (4) clustering of SES.MPD, SES.PD and SES.MNTD.



**Fig. 5.** Error bars of diversity indices based on the coefficient of SARerr result (coefficients  $\pm$  SE).



**Fig. 6.** A: Map of Functional dispersion (FDis) of trees in Mediterranean Europe. B: Map of phylogenetic tree species variability PSVs in Mediterranean Europe. Area outside of Mediterranean Europe is coloured light grey.

month, and concentrated in eastern Spain, southern France, Corsica, southeast Sardinia, and North Macedonia in three Region “Southeastern, Southwestern, and Pelagonia”. In contrast, the standardized values (SES.PD and SES.MPD) were located in the low value of latitude and longitude “the southern part of the study area” (Fig. 3; Appendix S18). The cluster analysis of PCA results (Fig. 4) showed that the indices PD, FD, FDis and richness clustered together, opposite to the indices MPD, PSVs, MNTD, SES.MPD, SES.PD and SES.MNTD, which grouped together.

## DISCUSSION

### Is phylogenetic diversity a good surrogate of functional diversity in the Euro-Mediterranean tree community?

In our study, the relationships between phylogeny and functions distances were weak. These results are congruent with the

results of Cheikh Albassatneh *et al.* (2019) for genera of European Mediterranean trees, which also revealed a rather weak and marginally significant relationship between the distance matrices of phylogeny and life history traits.

Our results confirm no relationship between the phylogenetic species variability index (PSV) and functional dispersion (FDis). These results are congruent with Pavoine *et al.* (2013), who performed a field study in the coastal marsh plain of Mekhada, Algeria, in which they demonstrated that PD was a poor surrogate for FD, and also less correlated with environmental variables than FD, and that species richness was a better surrogate for FD than PD in identifying the ecological processes that distribute species along a salinity gradient. They concluded that FD and PD indices might correlate simply because variation in species richness and evenness (referred to as co-factors) influences both FD and PD values. According to several studies (Cianciaruso *et al.* 2012; Pavoine *et al.* 2013), the relationship between FD and PD is evolutionary and

functionally nonlinear and complex because the relationship is likely to be specific to the community and function studied, and traits do not necessarily evolve at the same rate (Donoghue 2008).

Despite the weak correlation between these two (phylogenetic and functional) distance matrices, we have demonstrated that the relationship between phylogenetic information and functional traits varies among traits according to the evolutionary (or divergence) scale considered. This context is perfect for investigating the nature of such links. Trait values tended to be similar for closely related species, demonstrating phylogenetic conservatism (see Kelly *et al.* 2014). In another example, Swenson & Enquist (2007) examined the evolutionary ecology of wood density using a large database for seed plants in the American Neotropics. In particular, they focused on the geographic and phylogenetic variation in wood density for both gymnosperms and angiosperms. They demonstrated that wood density was generally highly conserved across the entire seed plant phylogeny, yet large divergences were found within the Rosid clade.

In this study, we found that a pure Brownian motion model was not sufficient to explain the variation of each trait along the evolutionary distance gradient (time divergence) when the whole phylogeny was considered (Table 1). Nevertheless, applying the lambda statistics over the whole tree, our results also demonstrated that the phylogenetic signal changes in different time slices. In fact, our study showed that different traits did not vary similarly along an evolutionary distance gradient. For example, Moran's I of maximum height, stem specific density, and seed dry mass were found to be low at the largest divergence times (phylogenetic distance). For these traits, only closely related species shared similar values, and the phylogenetic signal was lost at larger divergences. For SLA and maximum plant height, the correlation decreased sharply around 400 Mya, *i.e.*, the divergence time between gymnosperms and angiosperms ( $385 \pm 72$  Mya, according to Zimmer *et al.* (2007)).

Our results can also help to define where and why phylogenetics could be used as a proxy for functional diversity, as underlined by Winter *et al.* (2013), as the four functional traits were shown to be important for forest conservation, and those traits were also shown to vary at different depths in evolutionary history. The phylogeny can be seen as a mixture of the effect of different traits evolving at different speeds and could be used as a proxy for functional diversity (Paquette *et al.* 2015). Phylogenetic information may still be used advantageously, in cases where data on traits are scarce or incomplete, to accelerate the investigation of biodiversity–ecosystem functioning relationships in undocumented ecosystems. Although specific relationships between functional diversity and phylogenetic diversity are likely context specific.

#### What are the environmental predictors of species richness, phylogenetic diversity and functional diversity?

We found that the several phylogenetic indices (MPD, PSVs, SES.MPD, SES.PD and SES.MNTD) were not correlated with species richness. However, MNTD was negatively correlated with species richness, as also shown by Miller *et al.* (2017). PSVs and MPD were strongly correlated, underlining that PSVs is actually analogous to MPD, and they just take different

routes to the same value (Cadotte & Davies 2016). The SES.MPD and SES.MNTD metrics used to measure within-site phylogenetic divergence yielded results with important differences that can be explained by the fact that these two metrics do not detect phylogenetic patterns at the same depth (Swenson 2011). According to previous studies (Losos 2008; Cavender-Bares *et al.* 2009), phylogenetic structures within communities vary according to the phylogenetic signal in functional traits and habitat association, which in turn varies with the phylogenetic depth. In our study, the degree of clustering was found to be stronger with SES.MNTD (Fig. 3) which, unlike SES.MPD, is a terminal metric detecting patterns near the tips of the trees. This result is consistent with our knowledge of niche evolution of northeastern American forests, as it has been shown that the phylogenetic signal for many ecological optima is mainly located at lower phylogenetic levels (Paquette *et al.* 2015).

Our study revealed a highly non-random spatial and environmental distribution of phylogenetic diversity (PD) across tree communities of the Mediterranean area in Europe across all metrics used, with some areas and environments holding significantly more (or less) phylogenetic diversity than others (Appendix S16 and S17). Phylogenetic diversity (PD) and functional diversity (FD, FDis) of Mediterranean forest trees in Europe correlated strongly with species richness (SR). High values of these indices were located in the north of the study area and positively influenced by altitude, and minimum temperature of the coldest month. Conversely, the low values of these indices were located in the south of the studied area and at low altitudes.

In contrast, the two phylogenetic indices that were not correlated with species richness (MPD, PSVs) were positively correlated with low latitude “south of area”, soil organic carbon stock (OMS) and sandy soil texture. The highest value of these two indices was situated at the high altitude of the study area. These results are incongruent with results of Qian *et al.* (2013). They tested two predictions of the phylogenetic niche conservatism hypothesis for the latitudinal diversity gradient of angiosperm trees in North America: (1) species in colder regions tend to show a greater phylogenetic clustering than those in warmer regions, and (2) clades are younger in colder regions. They demonstrated that species richness and mean clade age were negatively correlated with latitude and positively correlated with minimum temperature. This difference between the two studies is because the climate of Canada and Alaska is Subarctic and Boreal, with winter “freezing temperatures” unfavourable for specific richness (Latham & Ricklefs 1993; Wiens & Donoghue 2004; Qian *et al.* 2013), whereas the climate of the northern part of Mediterranean region is dominated by (i) mountain Mediterranean trees, where the principal vegetation is the upland coniferous forests with *Pinus nigra*, in addition to Mediterranean firs and cedars, and (ii) supra-Mediterranean trees, as illustrated by the deciduous oak forests, dominated in the humid bioclimate with *Ostrya* and *Carpinus*, and sclerophyllous oaks (Thompson 2005).

#### Conclusions and perspectives

We provide, for the first time, a species-level phylogeny of the 203 tree species of the European Mediterranean region. Despite

limited studies in the field of spatial community phylogenetics, the rapid increase in availability of molecular phylogenies and fine species distribution data make it possible for ecologists to start to estimate a proxy of biodiversity ecosystem functioning effects, their direction, strength and shape. This is important, as we lack functional trait descriptions for many organisms of less studied ecosystems, functions or services, and even more so for Mediterranean ecosystems, especially in the eastern Mediterranean Basin that has undergone human impacts since the ancient past (Rundel & Cowling 2013).

## AUTHOR CONTRIBUTIONS

MCA: methodology, data curation, data analysis, original draft preparation, writing, editing, ME: methodology, original draft preparation, writing, reviewing, BF: original draft preparation, writing, reviewing and correction of English, LP: methodology, reviewing, J-YD: original draft preparation, reviewing, SM: original draft preparation, reviewing. All authors took part in the conceptualization of the work and have read and approved the final version of the manuscript.

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## SUPPORTING INFORMATION

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

**Appendix S1.** List of 203 species using additional taxa from the main clades and orders of gymnosperms, angiosperms and ferns to infer an extended tree that contains the main clades and orders.

**Appendix S2.** DNA\_BARCODE\_all\_genes\_277.xlsx. All available sequence data for our target taxa from NCBI and from the datasets of Monnet *et al.* (2021).

**Appendix S3.** seq\_all\_genes\_277.nexus. The supermatrix of 277 species and 11,722 sites.

**Appendix S4.** best\_tree\_RAxML\_277.tre. The best tree of the 277 species using RAxML. The GTRGAMMA nucleotide substitution model was used for all partitions.

**Appendix S5.** edge\_null\_tree\_277\_from\_v.phyloMaker.txt.txt. The constraint tree option using a backbone tree using edge null tree of 277 species from *V. phyloMaker*, scenario 3 (Jin & Qian 2019).

**Appendix S6.** 100\_trees278\_sunplin.nexus. Simulation with Uncertainty for Phylogenetic Investigating (SUNPLIN) implemented in R, using the branch-based method as random insertion (Martins *et al.* 2013).

**Appendix S7.** tree278\_10\_notnoded.tree. The phylogenetic tree File used to estimate a chronogram of 278 species.

**Appendix S8.** treePL\_config.txt. The treePL configuration file for estimating the chronogram of 278 species using the software *treePL* (Smith & O'Meara 2012) with 42 calibration points from the literature (Magallón *et al.* 2013; Rothfels *et al.* 2015).

**Appendix S9.** GC.ultrametric\_dated\_tree\_species\_278-tre.pdf. Ultrametric dated tree.

**Appendix S10.** Dropped\_DATED\_TREE203.tree.

**Appendix S11.** Variables.doc. Full list of variables considered in the analysis of Mediterranean trees in Europe.

**Appendix S12.** Tanglogram.pdf. Tanglegram computing the phylogenetic tree (left) and the tree for functional traits (right) of the 188 tree species of Mediterranean Europe (row with missing value has been deleted).

**Appendix S13.** bouble\_size198sp.pdf. Standardized values (bubble size and shade) of the functional traits along the maximum phylogeny of the 203 tree species of Mediterranean Europe.

**Appendix S14.** Local\_moran\_indices.pdf. Local Moran's index ( $I_i$ ) values for each species (local indicator of phylogenetic association, LIPA) for each trait: Plant maximum height "Height", Seed dry mass "SeedMass", Leaf area per leaf dry mass "SLA", and Stem specific density "StemSpecDens". Red bars indicate significant  $I_i$  values ( $P < 0.05$ ), indicating phylogenetic signal. The figure demonstrates that significant local autocorrelation is concentrated, for example, for Plant maximum height "Height", within Pinaceae, *Ulmus*, *Fagus* and *Tilia*, and these significant values of  $I_i$  are positive, meaning that these species are positively autocorrelated (*e.g.* more similar to each other than would be expected due to random processes).

**Appendix S15.** Spearman\_correlation\_diversity\_indices.pdf. Relationship between phylogenetic and functional diversity using Spearman correlation.

**Appendix S16.** SARerr\_variables\_Histogram.docx. Best spatial autoregressive error models (SARerr) for the relationships among FD, Richness, SES.MPD, FDis, PD, SES.FDis, MPD, PSVs, SES.PD, MNTD and SES.MNTD and the predictor variables. Elevation (Alt), Temperature seasonality (T\_seasonality), Minimum temperature of the coldest month (T\_min\_coldest\_m), Total annual precipitation (P\_ann), Precipitation of driest month (P\_Dreist\_m), Ca<sup>+</sup> in water (Ca<sup>+</sup>), pH in water (pH), Soil organic carbon stock (OMS), Texture class (Texture\_class). Only the statistically significant variables are shown.

**Appendix S17.** SARerr\_variables\_table.docx. Best spatial autoregressive error models (SARerr) for the relationships among FD, Richness, SES.MPD, FDis, PD, SES.FDis, MPD, PSVs, SES.PD, MNTD and SES.MNTD and the predictor variables. AIC: Akaike Information criterion. Asterisks denote: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05. Elevation (Alt), Temperature seasonality (T\_seasonality), Minimum temperature of the coldest month (T\_min\_coldest\_m), Total annual precipitation (P\_ann), Precipitation of driest month (P\_Dreist\_m), Ca<sup>+</sup> in water (Ca<sup>+</sup>), pH in water (pH), Soil organic carbon stock (OMS), Texture class (Texture\_class). Only the statistically significant variables are shown.

**Appendix S18.** alpha\_diversity\_maps.docx. Maps of alpha diversity indices.



## REFERENCES

- Abouheif E. (1999) A method for testing the assumption of phylogenetic independence in comparative data. *Evolutionary Ecology Research*, **1**, 895–909.
- Aurelle D., Thomas S., Albert C., Bally M., Bondeau A., Boudouresque C.-F., Cahill A.E., Carlotti F., Chenuil A., Cramer W., Davi H., De Jode A., Ereskovsky A., Farnet A.-M., Fernandez C., Gauquelin T., Mirleau P., Monnet A.-C., Prévosto B., Rossi V., Sartoretto S., Van Wambeke F., Fady B. (2022) Biodiversity, climate change, and adaptation in the Mediterranean. *Ecosphere*, **13**, e3915. <https://doi.org/10.1002/ecs2.3915> accessed 23 September 2022.
- Ben-Hur E., Fragman-Sapir O., Hadas R., Singer A., Kadmon R. (2012) Functional trade-offs increase species diversity in experimental plant communities. *Ecology Letters*, **15**, 1276–1282.
- Bivand R., Anselin L., Berke O., Bernat A., Carvalho M., Chun Y., Dormann C., Dray S., Halbersma R., Lewin-Koh N. (2006) *Spdep: spatial dependence: Weighting schemes, statistics and models*. Package in R.
- Bucharova A., Van Kleunen M. (2009) Introduction, history and species characteristics partly explain naturalization success of north American woody species in Europe. *Journal of Ecology*, **97**, 230–238. <https://doi.org/10.1111/j.1365-2745.2008.01469.x> accessed 9 September 2021.
- Cadotte M.W., Carscadden K., Mirotchnick N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x> accessed 19 January 2020.
- Cadotte M.W., Cavender-Bares J., Tilman D., Oakley T.H. (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS One*, **4**, e5695. <https://doi.org/10.1371/journal.pone.0005695>
- Cadotte M.W., Davies T.J. (2016) *Phylogenies in ecology: a guide to concepts and methods*. Princeton University Press, Princeton, NJ, USA.
- Cardinale B.J., Matulich K.L., Hooper D.U., Byrnes J.E., Duffy E., Gamfeldt L., Balvanera P., O'Connor M.I., Gonzalez A. (2011) The functional role of producer diversity in ecosystems. *American Journal of Botany*, **98**, 572–592. <https://doi.org/10.3732/ajb.1000364> accessed 10 December 2020.
- Cardinale B.J., Srivastava D.S., Emmett Duffy J., Wright J.P., Downing A.L., Sankaran M., Jouseau C. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989–992. <https://doi.org/10.1038/nature05202>
- Castresana J. (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, **17**, 540–552.
- Cavender-Bares J., Kozak K.H., Fine P.V., Kembel S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.
- Chave J., Coomes D., Jansen S., Lewis S.L., Swenson N.G., Zanne A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
- Cheikh Albassatneh M., Escudero M., Monnet A.-C., Arroyo J., Bacchetta G., Bagnoli F., Dimopoulos P., Hampe A., Leriche A., Médail F., Nikolic T., Ponger L., Vendramin G.G., Fady B. (2021) Spatial patterns of genus-level phylogenetic endemism in the tree flora of Mediterranean Europe. *Diversity and Distributions*, **27**, 913–928. <https://doi.org/10.1111/ddi.13241> accessed 1 June 2021.
- Cheikh Albassatneh M., Escudero M., Ponger L., Monnet A.-C., Arroyo J., Nikolic T., Bacchetta G., Bagnoli F., Dimopoulos P., Leriche A., Médail F., Roig A., Spanu I., Vendramin G.G., Hampe A., Fady B. (2019) A comprehensive, genus-level time-calibrated phylogeny of the tree flora of Mediterranean Europe and an assessment of its vulnerability. *Botany Letters*, **167**, 276–289. <https://doi.org/10.1080/23818107.2019.1684360>
- Chiu C.-H., Chao A. (2014) Distance-based functional diversity measures and their decomposition: a framework based on hill numbers. *PLoS One*, **9**, e100014.
- Cianciaruso M.V., Silva I.A., Batalha M.A., Gaston K.J., Petchey O.L. (2012) The influence of fire on phylogenetic and functional structure of woody savannas: moving from species to individuals. *Perspectives in Plant Ecology, Evolution and Systematics*, **14**, 205–216.
- Cock P.J.A., Antao T., Chang J.T., Chapman B.A., Cox C.J., Dalke A., Friedberg I., Hamelryck T., Kauff F., Wilczynski B., de Hoon M.J.L. (2009) Biopython: freely available python tools for computational molecular biology and bioinformatics. *Bioinformatics*, **25**, 1422–1423. <https://doi.org/10.1093/bioinformatics/btp163> accessed 14 December 2020.
- Cornelissen J., Lavorel S., Garnier E., Diaz S., Buchmann N., Gurvich D., Reich P., Ter Steege H., Morgan H., Van Der Heijden M. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.
- Darriba D., Taboada G.L., Doallo R., Posada D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, **9**, 772. <https://doi.org/10.1038/nmeth.2109>
- Diaz S., Cabido M. (2001) Vive la différence: plant functional diversity matters to ecosystem functioning. *Trends in Ecology & Evolution*, **16**, 646–655.
- Diaz S., Lavorel S., de Bello F., Quétier F., Grigulis K., Robson T.M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 20684. <http://www.pnas.org/content/104/52/20684.abstract>
- Donoghue M.J. (2008) A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11549–11555.
- Donovan L.A., Maherali H., Caruso C.M., Huber H., de Kroon H. (2011) The evolution of the worldwide leaf economics spectrum. *Trends in Ecology & Evolution*, **26**, 88–95.
- Faith D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10. <http://www.sciencedirect.com/science/article/pii/0006320792912013>
- Felsenstein J. (1973) Maximum likelihood and minimum-steps methods for estimating evolutionary trees from data on discrete characters. *Systematic Zoology*, **22**, 240–249. <http://www.jstor.org/stable/2412304>
- Fick S.E., Hijmans R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, **37**, 4302–4315. <https://doi.org/10.1002/joc.5086> accessed 18 May 2021.
- Flynn D.F.B., Mirotchnick N., Jain M., Palmer M.I., Naem S. (2011) Functional and phylogenetic diversity as predictors of biodiversity–ecosystem–function relationships. *Ecology*, **92**, 1573–1581. <https://doi.org/10.1890/10-1245.1> accessed 6 May 2019.
- Forest F., Grenyer R., Rouget M., Davies J., Cowling R., Faith D., Balmford A., Manning J., Procheş Ş., Bank M., Reeves G., Hedderson T., Savolainen V. (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, **445**, 757–760.
- Fox J., Weisberg S. (2019) *An R companion to applied regression*, 3rd edition. Sage, Thousand Oaks, CA, USA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Freckleton R.P., Harvey P.H., Pagel M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **160**, 712–725.
- Freyman W.A., Thornhill A.H. (2016) *Matrix maker* [Computer software]. <https://github.com/wf8/matrixmaker>
- Gaston K. (1996) Species richness: measures and measurements. In: Gaston K.J. (Ed), *Biodiversity: a biology of numbers and differences*. Blackwell Science, Oxford, UK, pp 77–113.
- Gittleman J.L., Kot M. (1990) Adaptation: statistics and a null model for estimating phylogenetic effects. *Systematic Zoology*, **39**, 227–241. <http://www.jstor.org/stable/2992183>
- Gotelli N., Mccabe D. (2002) Species Co-occurrence: a meta-analysis of J. M. Diamond's Assembly Rules Model. *Ecology*, **83**, 2091–2096.
- Gower J.C. (1971) A general coefficient of similarity and some of its properties. *Biometrics*, **27**, 857–871.
- Hackathorn R., Bolker B., Butler M., Cowan P., Vienne D., Eddelbuettel D. (2011) *Phylobase: base package for phylogenetic structures and comparative data*. Package in R version 0.6.3.
- Hájek M., Jiménez-Alfaro B., Hájek O., Brancaloni L., Cantóni M., Carbognani M., Dedić A., Ditě D., Gerdol R., Hájková P., Horsakova V., Jansen F., Kamberović J., Kapfer J., Kolari T., Lamentowicz M., Lazarevic P., Mašić E., Moeslund J., Horsák M. (2021) A European map of groundwater pH and calcium. *Earth System Science Data*, **13**, 1089–1105.
- Hamilton M.A., Murray B.R., Cadotte M.W., Hose G.C., Baker A.C., Harris C.J., Licari D. (2005) Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters*, **8**, 1066–1074. <https://doi.org/10.1111/j.1461-0248.2005.00809.x> accessed 9 September 2021.
- Hardy O.J., Pavoine S. (2012) Assessing phylogenetic signal with measurement error: a comparison of Mantel tests, Blomberg et al.'s K, and phylogenetic distograms. *Evolution*, **66**, 2614–2621. <https://doi.org/10.1111/j.1558-5646.2012.01623.x> accessed 12 January 2023.
- Harmon L.J., Weir J.T., Brock C.D., Glor R.E., Challenger W. (2008) GEIGER: investigating evolutionary radiations. *Bioinformatics*, **24**, 129–131. <https://doi.org/10.1093/bioinformatics/btm538> accessed 9 February 2021.
- Helmus M.R., Bland T.J., Williams C.K., Ives A.R. (2007) Phylogenetic measures of biodiversity. *The American Naturalist*, **169**, E68–E83.
- Hengl T., Mendes de Jesus J., Heuvelink G.B.M., Ruiperez Gonzalez M., Kilibarda M., Blagotić A., Shangguan W., Wright M.N., Geng X., Bauer-Marschallinger B., Guevara M.A., Vargas R., MacMillan R.A., Batjes N.H., Leenaars J.G.B., Ribeiro E.,

- Wheeler I., Mantel S., Kempen B. (2017) Soil-Grids250m: global gridded soil information based on machine learning. *PLoS One*, **12**, e0169748. <https://doi.org/10.1371/journal.pone.0169748>
- Hijmans R., Van Etten J., Cheng J., Mattiuzzi M., Sumner M., Greenberg J., Lamigueiro O.P., Bevan A., Racine E., Shortridge A. (2016) *Package 'raster'*. Package in R.
- Hooper D.U., Chapin F.S., III, Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H., Lodge D.M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A.J., Vandermeer J., Wardle D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35. <http://pubs.er.usgs.gov/publication/1016580>
- Jensen K., Gutekunst K. (2003) Effects of litter on establishment of grassland plant species: the role of seed size and successional status. *Basic and Applied Ecology*, **4**, 579–587. <https://www.sciencedirect.com/science/article/pii/S1439179104701516>
- Jin Y., Qian H. (2019) V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography*, **42**, 1353–1359. <https://doi.org/10.1111/ecog.04434> accessed 15 May 2020.
- Joly S., Davies T.J., Archambault A., Bruneau A., Derry A., Kembel S.W., Peres-Neto P., Vamوسي J., Wheeler T.A. (2014) Ecology in the age of DNA barcoding: the resource, the promise and the challenges ahead. *Molecular Ecology Resources*, **14**, 221–232.
- Jombart T., Balloux F., Dray S. (2010) Apephylo: new tools for investigating the phylogenetic signal in biological traits. *Bioinformatics*, **26**, 1907–1909. <https://doi.org/10.1093/bioinformatics/btq292> accessed 17 May 2019.
- Katoh K., Misawa K., Kuma K., Miyata T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, **30**, 3059–3066. <https://doi.org/10.1093/nar/gkf436> accessed 13 January 2023.
- Keck F., Rimet F., Bouchez A., Franc A. (2016) Phylo-signal: an R package to measure, test, and explore the phylogenetic signal. *Ecology and Evolution*, **6**, 2774–2780. <https://doi.org/10.1002/ece3.2051> accessed 21 January 2023.
- Kelly S., Grenyer R., Scotland R.W. (2014) Phylogenetic trees do not reliably predict feature diversity. *Diversity and Distributions*, **20**, 600–612.
- Kembel S.W., Cowan P.D., Helmus M.R., Cornwell W.K., Morlon H., Ackerly D.D., Blomberg S.P., Webb C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166> accessed 16 May 2019.
- Kembel S.W., Cahill J.F., Jr. (2011) Independent evolution of leaf and root traits within and among temperate grassland plant communities. *PLoS One*, **6**, e19992.
- Kissling W.D., Carl G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography*, **17**, 59–71. <https://doi.org/10.1111/j.1466-8238.2007.00334.x> accessed 13 May 2021.
- Kuhner M.K., Felsenstein J. (1994) A simulation comparison of phylogeny algorithms under equal and unequal evolutionary rates. *Molecular Biology and Evolution*, **11**, 459–468. <https://doi.org/10.1093/oxfordjournals.molbev.a040126> accessed 6 May 2019.
- Laliberté E., Legendre P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.
- Laliberté E., Legendre P., Shipley B., Laliberté M. (2014) *Measuring functional diversity from multiple traits, and other tools for functional ecology*. R Package FD.
- Latham R.E., Ricklefs R.E. (1993) Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos*, **67**, 325–333. <http://www.jstor.org/stable/3545479> accessed 2 September 2021.
- Lavergne S., Thompson J.D., Garnier E., Debussche M. (2004) The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos*, **107**, 505–518. <https://doi.org/10.1111/j.0030-1299.2004.13423.x> accessed 9 September 2021.
- Lê S., Josse J., Husson F. (2008) FactoMineR: a package for multivariate analysis. *Journal of Statistical Software*, **25**, 1–18.
- Legendre P., Legendre L. (1998) *Numerical ecology*, 2nd edition. Elsevier, Amsterdam, Netherlands.
- Legendre P., Legendre L. (2012) *Numerical ecology*. Elsevier, Amsterdam, Netherlands.
- Losos J. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, **11**, 995–1003.
- Mace G., Cramer W., Diaz S., Faith D., Larigauderie A., Le Prestre P., Palmer M., Perrings C., Scholes R., Walpole M., Walther B., Watson J., Mooney H. (2010) Biodiversity targets after 2010. *Current Opinion in Environmental Sustainability*, **2**, 3–8.
- Magallón S., Hilu K.W., Quandt D. (2013) Land plant evolutionary timeline: gene effects are secondary to fossil constraints in relaxed clock estimation of age and substitution rates. *American Journal of Botany*, **100**, 556–573. <https://doi.org/10.3732/ajb.1200416> accessed 23 October 2018.
- Manly B., Sanderson J.G. (2002) A note on null models: justifying the methodology. *Ecology*, **83**, 580–582. <http://www.jstor.org/stable/2680037> accessed 6 April 2021.
- Mantel N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research*, **27**, 209–220. [http://cancerres.aacrjournals.org/content/27/2\\_Part\\_1/209.abstract](http://cancerres.aacrjournals.org/content/27/2_Part_1/209.abstract)
- Martins W.S., Carmo W.C., Longo H.J., Rosa T.C., Rangel T.F. (2013) SUNPLIN: simulation with uncertainty for phylogenetic investigations. *BMC Bioinformatics*, **14**, 324. <https://doi.org/10.1186/1471-2105-14-324>
- McMahon M.M., Sanderson M.J. (2006) Phylogenetic supermatrix analysis of GenBank sequences from 2228 papilionoid legumes. *Systematic Biology*, **55**, 818–836. <https://doi.org/10.1080/10635150600999150>
- Médail F., Monnet A.-C., Pavon D., Nikolic T., Dimopoulos P., Bacchetta G., Arroyo J., Barina Z., Albassatneh M.C., Domina G., Fady B., Matevski V., Misfud S., Leriche A. (2019) What is a tree in the Mediterranean Basin hotspot? A critical analysis. *Forest. Ecosystems*, **6**, 17–19. <https://doi.org/10.1186/s40663-019-0170-6>
- Miller E.T., Farine D.R., Trisos C.H. (2017) Phylogenetic community structure metrics and null models: a review with new methods and software. *Ecography*, **40**, 461–477.
- Mokany K., Ash J., Roxburgh S. (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893. <https://doi.org/10.1111/j.1365-2745.2008.01395.x> accessed 21 September 2019.
- Monnet A.-C., Cilleros K., Médail F., Albassatneh M.C., Arroyo J., Bacchetta G., Bagnoli F., Barina Z., Cartereau M., Casajus N., Dimopoulos P., Domina G., Doxa A., Escudero M., Fady B., Hampe A., Matevski V., Misfud S., Nikolic T., Pavon D., Roig A., Barea E.S., Spanu I., Strid A., Vendramin G.G., Leriche A. (2021) WOODIV, a database of occurrences, functional traits, and phylogenetic data for all Euro-Mediterranean trees. *Scientific Data*, **8**, 89. <https://doi.org/10.1038/s41597-021-00873-3>
- Moran P.A.P. (1950) Notes on continuous stochastic phenomena. *Biometrika*, **37**, 17–23. <http://www.jstor.org/stable/2332142>
- Mouchet M.A., Villéger S., Mason N.W., Moullot D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**, 867–876.
- Münkemüller T., Lavergne S., Bzeznik B., Dray S., Jombart T., Schifffers K., Thuiller W. (2012) How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, **3**, 743–756.
- Naeem S., Duffy J.E., Zavaleta E. (2012) The functions of biological diversity in an age of extinction. *Science*, **336**, 1401–1406. <http://science.sciencemag.org/content/336/6087/1401.abstract>
- Norberg J., Swaney D.P., Dushoff J., Lin J., Casagrandi R., Levin S.A. (2001) Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 11376–11381.
- Oksanen J., Simpson G., Blanchet F.G., Kindt R., Legendre P., Minchin P., Hara R., Solymos P., Stevens H., Szöcs E., Wagner H., Barbour M., Bedward M., Bolker B., Borcard D., Carvalho G., Chirico M., De Cáceres M., Durand S., Weedon J. (2022) *Vegan community ecology package version 2.6–2 April 2022*. Package in R.
- Pagel M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884. <https://doi.org/10.1038/44766>
- Paquette A., Joly S., Messier C. (2015) Explaining forest productivity using tree functional traits and phylogenetic information: two sides of the same coin over evolutionary scale? *Ecology and Evolution*, **5**, 1774–1783. <https://www.ncbi.nlm.nih.gov/pubmed/26140194>
- Paquette A., Messier C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180. <https://doi.org/10.1111/j.1466-8238.2010.00592.x> accessed 22 September 2019.
- Paradis E., Claude J., Strimmer K. (2004) *APE: analyses of phylogenetics and evolution in R language*. Package in R.
- Pavoine S., Baguette M., Bonsall M.B. (2010) Decomposition of trait diversity among the nodes of a phylogenetic tree. *Ecological Monographs*, **80**, 485–507.
- Pavoine S., Gasc A., Bonsall M.B., Mason N.W. (2013) Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes? *Journal of Vegetation Science*, **24**, 781–793.
- Pavoine S., Ollier S., Pontier D., Chessel D. (2008) Testing for phylogenetic signal in phenotypic traits: new matrices of phylogenetic proximities. *Theoretical Population Biology*, **73**, 79–91. <http://www.sciencedirect.com/science/article/pii/S0040580907001177>

- Penny D., Henny M.D. (1985) The use of tree comparison metrics. *Systematic Zoology*, **34**, 75–82. <http://www.jstor.org/stable/2413347>
- Perronne R., Mauchamp L., Mouly A., Gillet F. (2014) Contrasted taxonomic, phylogenetic and functional diversity patterns in semi-natural permanent grasslands along an altitudinal gradient. *Plant Ecology and Evolution*, **147**, 165–175. <https://hal.archives-ouvertes.fr/hal-01074588>
- Petchey O.L., Gaston K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, **5**, 402–411.
- Petchey O.L., Gaston K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758. <https://doi.org/10.1111/j.1461-0248.2006.00924.x> accessed 11 January 2023.
- Petchey O.L., Gaston K.J. (2007) Dendrograms and measuring functional diversity. *Oikos*, **116**, 1422–1426.
- Petchey O.L., Hector A., Gaston K.J. (2004) How do different measures of functional diversity perform? *Ecology*, **85**, 847–857. <https://doi.org/10.1890/03-0226> accessed 10 December 2020.
- Podani J. (1999) Extending Gower's general coefficient of similarity to ordinal characters. *Taxon*, **48**, 331–340. <https://doi.org/10.2307/1224438> accessed 6 April 2021.
- Poos M.S., Walker S.C., Jackson D.A. (2009) Functional-diversity indices can be driven by methodological choices and species richness. *Ecology*, **90**, 341–347.
- Qian H., Zhang Y., Zhang J., Wang X. (2013) Latitudinal gradients in phylogenetic relatedness of angiosperm trees in North America. *Global Ecology and Biogeography*, **22**, 1183–1191. <https://doi.org/10.1111/geb.12069> accessed 19 August 2021.
- Quézel P., Médail F. (2003) *Ecologie et biogéographie des forêts du bassin méditerranéen*. Elsevier (Collection Environnement), Paris, France.
- R Core Team (2020) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Reich P.B., Walters M.B., Ellsworth D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 13730–13734.
- Reiss J., Bridle J.R., Montoya J.M., Woodward G. (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution*, **24**, 505–514. <http://www.sciencedirect.com/science/article/pii/S0169534709001803>
- Revell L.J. (2012) Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223. <https://doi.org/10.1111/j.2041-210X.2011.00169.x> accessed 17 May 2019.
- Ricotta C. (2005) A note on functional diversity measures. *Basic and Applied Ecology*, **6**, 479–486.
- Rodrigues A.S.L., Grenyer R., Baillie J.E.M., Bininda-Emonds O.R.P., Gittlemann J.L., Hoffmann M., Safi K., Schipper J., Stuart S.N., Brooks T. (2011) Complete, accurate, mammalian phylogenies aid conservation planning, but not much. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **366**, 2652–2660. <https://www.ncbi.nlm.nih.gov/pubmed/21844044>
- Rothfels C.J., Li F.-W., Sigel E.M., Huiet L., Larsson A., Burge D.O., Ruhsam M., Deyholos M., Soltis D.E., Stewart C.N.J., Shaw S.W., Pokorny L., Chen T., dePamphilis C., DeGironimo L., Chen L., Wei X., Sun X., Korall P., Stevenson D.W., Graham S.W., Wong G.K.-S., Pryer K.M. (2015) The evolutionary history of ferns inferred from 25 low-copy nuclear genes. *American Journal of Botany*, **102**, 1089–1107.
- Rundel P., Cowling R. (2013) Mediterranean-climate ecosystems, *Encyclopedia of biodiversity*, 2nd edition. Elsevier, Amsterdam, Netherlands, pp 212–222.
- Sanderson M.J., Ané C., Eulenstein O., Fernández-Baca D., Kim J., McMahon M.M., Piaggio-Talice R. (2007) Fragmentation of large data sets in phylogenetic analyses. In: Gascuel O., Steel M. (Eds), *Reconstructing evolution: new mathematical and computational advances*. Oxford, UK. <https://www.amazon.com/Reconstructing-Evolution-Mathematical-Computational-Advances/dp/0199208220>
- Satdichanh M., Millet J., Heinemann A., Nanthavong K., Harrison R.D. (2015) Using plant functional traits and phylogenies to understand patterns of plant community assembly in a seasonal tropical forest in Lao PDR. *PLoS One*, **10**, e0130151. <https://doi.org/10.1371/journal.pone.0130151>
- Schmera D., Erős T., Podani J. (2009) A measure for assessing functional diversity in ecological communities. *Aquatic Ecology*, **43**, 157–167.
- Shangguan W., Hengl T., Mendes de Jesus J., Yuan H., Dai Y. (2017) Mapping the global depth to bedrock for land surface modeling. *Journal of Advances in Modeling Earth Systems*, **9**, 65–88. <https://doi.org/10.1002/2016MS000686> accessed 18 May 2021.
- Smith S.A., O'Meara B.C. (2012) treePL: divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics (Oxford, England)*, **28**, 2689–2690.
- Srivastava D.S., Cadotte M.W., MacDonald A.A.M., Marushia R.G., Mirotnich N. (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters*, **15**, 637–648. <https://doi.org/10.1111/j.1461-0248.2012.01795.x> accessed 4 May 2019.
- Stamatakis A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, **30**, 1312–1313. <http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3998144/>
- Steel M.A., Penny D. (1993) Distributions of tree comparison metrics—Some new results. *Systematic Biology*, **42**, 126–141. <https://doi.org/10.1093/sysbio/42.2.126> accessed 6 May 2019.
- Suding K.N., Lavorel S., Chapin I.F., Cornelissen J.H., Diaz S., Garnier E., Goldberg D., Hooper D.U., Jackson S.T., Navas M. (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125–1140.
- Swenson N. (2011) Phylogenetic Beta diversity metrics, trait evolution and inferring the functional Beta diversity of communities. *PLoS One*, **6**, e21264.
- Swenson N.G. (2012) The functional ecology and diversity of tropical tree assemblages through space and time: from local to regional and from traits to transcriptomes. *International Scholarly Research Notices*, **2012**, 743617.
- Swenson N.G., Enquist B.J. (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, **94**, 451–459.
- Swenson N.G., Erickson D.L., Mi X., Bourg N.A., Forero-Montaña J., Ge X., Howe R., Lake J.K., Liu X., Ma K. (2012) Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. *Ecology*, **93**, S112–S125.
- Thompson J. (2005) *Plant evolution in the Mediterranean*. Oxford University Press, New York, NY, USA.
- Tiefelsdorf M., Griffith D.A., Boots B. (1999) A variance-stabilizing coding scheme for spatial link matrices. *Environment and Planning A: Economy and Space*, **31**, 165–180. <https://doi.org/10.1068/a310165> accessed 13 May 2021.
- Tilman D. (2001) Functional diversity. *Encyclopedia of Biodiversity*, **3**, 109–120.
- Van Rossum G., Drake F.L. (2009) *Python 3 reference manual*. CreateSpace, Scotts Valley, CA.
- Villéger S., Mason N.W., Moullot D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301.
- Walker B., Kinzig A., Langridge J. (1999) Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, **2**, 95–113.
- Warnes G.R., Bolker B., Lumley T. (2015) *gtools: various R Programming Tools*. R package version 3.5.0. <https://CRAN.R-project.org/package=gtools#suberufen>
- Webb C.O., Ackerly D.D., McPeck M.A., Donoghue M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448> accessed 4 May 2019.
- Wiens J.J., Donoghue M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, **19**, 639–644. <https://www.sciencedirect.com/science/article/pii/S0169534704002745>
- Winter M., Devictor V., Schweiger O. (2013) Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology & Evolution*, **28**, 199–204. <https://www.sciencedirect.com/science/article/pii/S0169534712002881>
- Wright I.J., Reich P.B., Westoby M., Ackerly D.D., Baruch Z., Bongers F., Cavender-Bares J., Chapin T., Cornelissen J.H., Diemer M. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Zimmer A., Lang D., Richardt S., Frank W., Reski R., Rensing S.A. (2007) Dating the early evolution of plants: detection and molecular clock analyses of orthologs. *Molecular Genetics and Genomics*, **278**, 393–402.