



## Beyond taxonomic diversity: Revealing spatial mismatches in phylogenetic and functional diversity facets in Mediterranean tree communities in southern France



Aggeliki Doxa<sup>a,b,\*</sup>, Vincent Devictor<sup>c</sup>, Alex Baumel<sup>a</sup>, Daniel Pavon<sup>a</sup>, Frédéric Médail<sup>a</sup>, Agathe Leriche<sup>a</sup>

<sup>a</sup> Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale, Aix Marseille Univ, Avignon Univ, CNRS, IRD, IMBE, Technopôle de l'Arbois-Méditerranée, BP 80, 13 545 Aix-en-Provence cedex 4, France

<sup>b</sup> Institute of Applied and Computational Mathematics, Foundation for Research and Technology-Hellas (FORTH), N. Plastira 100, Vassilika Vouton, GR - 700 13 Heraklion, Crete, Greece

<sup>c</sup> Institut des Sciences de l'Evolution, UMR 5554, Université Montpellier, CC065, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France

### ARTICLE INFO

#### Keywords:

Congruence analysis  
Morphology traits  
Rao index  
Regeneration traits  
Spatial autocorrelation  
Traits convergence

### ABSTRACT

Adopting a multifaceted approach of biodiversity is believed to capture different aspects of the ecosystem functioning and it is thus advised for conservation prioritisation, especially for anthropogenic ecosystems but this key topic has never been conducted for the Mediterranean tree assemblages, despite their ecological importance. We explored how the multi-faceted diversity of woody plant assemblages, as measured by taxonomic (TD), functional (FD) and phylogenetic (PD) diversities, are distributed over space in the French part of the Mediterranean biome, and to which extent they are spatially correlated to each other, in order to understand whether one facet can be used as a proxy for another, especially for conservation management purposes.

We analysed data from 5885 plots over the study area. We estimated several FD types by considering separately (i) regeneration, (ii) morphology traits (iii) modalities on species ecological properties, and finally (iv) considering all traits together. We used the Rao quadratic entropy to estimate the TD, FD and PD diversity facets. We tested for the links and spatial correlation (congruence) levels among these facets, using simultaneous autoregressive (SAR) models and partial Mantel tests.

Spatial structure varied among diversity facets and spatial autocorrelation patterns were identified for all diversity indices from 30 to 50 km distances. We observed a functional convergence and a phylogenetic divergence within tree assemblages comparing to the ones expected given the regional species pool, indicating that even in tree communities with functional similarities, phylogenetic diversity may be high. PD was zero to slightly congruent to FD, regardless the type of functional traits considered. The highest SAR slope ( $=0.3$ ) and partial Mantel test ( $=0.2$ ) were revealed between the PD and the FD based on species morphological traits, but still remained considerably low.

Each one of the diversity indicators reflected a different tree community spatial pattern. Functional diversity patterns varied according to the type of traits considered. Using only taxonomic indices may be misleading for responding to Mediterranean tree assemblages conservation needs and additional information about the species phylogeny and functional responses to disturbance pressures should be considered in large scale analyses.

### 1. Introduction

Functional diversity (FD) and phylogenetic diversity (PD) were recognized as important components of biodiversity, implying that an effective conservation strategy should rely on the maintenance of

species, functional and evolutionary processes in habitats at different scales, especially in face of global changes (Brooks et al., 2006). A growing number of studies are considering multiple facets of diversity simultaneously i.e. taxonomic (TD), functional (FD) and phylogenetic (PD) diversities instead of using unique descriptors (Devictor et al.,

\* Corresponding author at: Institute of Applied and Computational Mathematics, Foundation for Research and Technology-Hellas (FORTH), N. Plastira 100, Vassilika Vouton, GR - 700 13 Heraklion, Crete, Greece.

E-mail address: [aggeliki.doxa@iacm.forth.gr](mailto:aggeliki.doxa@iacm.forth.gr) (A. Doxa).

<https://doi.org/10.1016/j.foreco.2020.118318>

Received 16 March 2020; Received in revised form 3 June 2020; Accepted 8 June 2020

0378-1127/ © 2020 Elsevier B.V. All rights reserved.

2010; Hao et al., 2019; Nóbrega et al., 2019) to propose adapted conservation strategies. However, the extent of their spatial correlation, and whether one facet can be used as a proxy for another in a conservation goal are still unclear.

Functional and phylogenetic diversities are used as relevant proxies to estimate ecosystem functioning (Cadotte et al., 2008; Swenson, 2011) and as two complementary aspects of ecological importance on their own (Mouquet et al., 2012). Functional diversity integrates the variability of traits in species assemblages and, in a given habitat, high diversity in species functional traits is often considered as assuring stability through the coexistence of different strategies allowing more resilience in unpredictable environments (Cadotte et al., 2011). Phylogenetic diversity represents the amount of phylogenetic information present in species communities and has been proposed as a metric of conservation interest, to avoid neglecting areas that might host a low number of species but phylogenetically distinct ones (Mouquet et al., 2012; Tucker & Cadotte, 2013).

The necessity of taking into account one or multiple diversity facets for conservation purposes depends however on how well spatially correlated these facets to one another (Devictor et al., 2010; Mazel et al., 2014). High spatial correlations among diversity facets, also known as congruence, would indicate that one facet can be used as a surrogate for other diversity facets and it can reasonably be privileged when needing to designate conservation priorities. In the opposite case, lack or limited congruence indicates that complementary information is obtained by each diversity facet and that all diversity dimensions are needed to identify conservation areas (Mouillot et al., 2011).

Although methodologies for quantifying taxonomic and phylogenetic diversities are considerably straightforward, the functional diversity can be more complex, as decisions such as traits selection, their number and type may influence our capacity to functionally discriminate species (Laughlin, 2014). For plants, it is advised when possible, to use traits from multiple organs, like leaf, root or flowering traits, which are connected to basic plant mechanisms, like interception of light and nutrient resources, resistance to disturbance and competitive strength (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013; Laughlin, 2014). However, as traits that drive community composition processes are not always known, phylogenetic relatedness among species has been proposed as a surrogate for functional similarity (Webb et al., 2002; Carboni et al., 2013). The main arguments for the use of FD and PD in ecology and conservation is that while FD metrics can be considered as a subset of true functional diversity, based on a limited number of traits, PD is a well-established tool that benefit from up-to-date molecular methods (Pagel, 1999; Cadotte et al., 2011). However there is recent evidence that phylogenetic evolution is unable to capture all aspects of functional structure, especially along ecological and biogeographical gradients, even in cases where phylogenetic trait conservatism do exist (Meynard et al., 2011; Mason & Pavoine, 2013). The link between phylogenetic and functional diversity is thus now considered less straightforward than previously thought (Winter et al., 2013; Gerhold et al., 2015) and may depend on the considered traits.

Few studies have investigated the congruence of large-scale diversity patterns and their implications for conservation issues in the Mediterranean biome for plants and even less for woody trees assemblages (ex. Bernard-Verdier et al., 2013 for Mediterranean rangeland; Thuiller et al., 2014 for the Alps). Mediterranean forests compose an interesting example of spatially extensive habitats characterized by high diversity complexity related to heterogeneous biogeographical histories (Quézel & Médail, 2003), with an important taxonomic diversity of trees for a temperate biome (Médail et al., 2019). Nevertheless, no analysis on all three diversity facets has yet been done to disentangle the spatial pattern of the different diversity dimensions for Mediterranean tree communities at the large scale. In addition, Mediterranean species having evolved under various biogeographic pressures, i.e. long-term and large scale breaks in climatic and landscape conditions (Montoya et al., 2007; Fady & Conord, 2010), are

characterised by a variety of traits that are well documented, which makes it an interesting case study and permits the use of different types of traits to produce various functional diversity indices.

In the present study, we estimated the taxonomic, functional and phylogenetic diversity of tree species assemblages within the French Mediterranean biome. We considered an important number of commonly used traits ( $n = 15$ ), to adequately capture species differences. We separated functional traits in regeneration, morphology and ecological modalities to specifically estimate different types of functional diversity.

Given the number and the variety of traits, we expected that traits convergence (or divergence) will probably vary according to the functional diversity type. We also expected differences among the spatial patterns of the functional diversity types and accordingly various spatial correlations between functional and phylogenetic diversity. We use spatially detailed data, at 1 km resolution, which permits us to test spatial autocorrelation patterns and potentially propose more adapted data resolution to study Mediterranean tree species assemblages in similar analyses. We aim to: (1) examine the spatial structure of each facet, especially in terms of spatial autocorrelation, (2) after correcting for the autocorrelation patterns, we investigated whether the functional diversity facets are related to the phylogenetic diversity, independently of the taxonomic diversity, to understand which diversity facet, if not both, should complement taxonomic diversity.

## 2. Materials and methods

### 2.1. Study area and tree species survey data

We used the French delimitation of the Mediterranean forests, woodland and shrubs biome, as defined by Olson et al. (2001) based on previous biogeographical studies, vegetation type maps, floristic provinces and the distribution of representative groups of plants. The study area covers a surface of 67.000 km<sup>2</sup>, representing 10% of the total surface of France.

We used species presence and relative coverage data, available through the French National Institute of Geographic and Forestry Information (IGN). In a Geographic Information System, we extracted the data that corresponded to our study zone (Fig. 2a). The IGN uses a standardized method, by first mapping all forest areas at the national scale, then systematically selecting survey plots in a distance of 1 km one to another. Species inventories were realized between 2005 and 2014 in 5885 plots over the study area, each plot covering a 25 m diameter area (of 491 m<sup>2</sup>), within which all tree species are noted together with their estimated coverage over the sampled area, according to the Braun-Blanquet relative coverage scale (<http://inventaire-forestier.ign.fr/spip/>), which varies from 1 (< 5% of coverage) to 5 (75–100% coverage), as noted by the botanists during field work. We considered the survey plot as our unit scale and used it for further analysis and calculation of co-occurrence based indices.

We first defined an exhaustive list of all tree species present in the French Mediterranean region ( $N = 121$ ). Including exogenous species in our analysis might had increased TD, FD and PD values and might had led to false conclusions of higher diversity. However, the presence of exogenous species in a given ecosystem, may alter interactions among species, increase competition or even exclude already installed local species, leading to long-term biodiversity loss. Thus we decided to exclude exogenous species ( $N = 20$ ) from the present analysis. Among the 101 remaining species from the list, 18 species lack IGN (occurrence) data, because of their restricted distribution or their complete absence in the continental part of the Mediterranean France (Corsica is not considered in this analysis). A total of 83 tree species were finally considered in the analysis, 70 Angiosperm species and 13 Gymnosperm species (for species list see Appendix 1). The average numbers of tree species per plot was 7 [min = 1, max = 20] species, 5.5 [1,19] Angiosperm species and 2 [1,7] Gymnosperms species per plot.

**Table 1**

List of functional traits. FDr was estimated using the regeneration traits, FDM was estimated based on the morphology traits, FDe was estimated on the ecological properties and FDt was based on all traits.

Type of traits	Traits	Modalities
Regeneration	Sexuality	Monoecious, Dioecious, Hermaphodite, Polygamous
	Pollination	Anemogamous, Entomogamous
	Bloom	Winter, Spring, Summer, Automne
	Fructification	Summer, Automne
	Dispersal	Anemochorous, Zoochorous, Barochorous
Morphology	Height	Small (< 5m), Medium (5–10 m), High (10–25 m), Very high (> 25 m)
	Life of leaves	Deciduous, Marcescent, Evergreen
	Shape of leaves	Acicular, Scale, Lauriforme, Malacophyllous, Microphyllous, Sclerophyllous
	Thorniness	with or without thorns
	Hairy leaves	with or without hairy leaves
	Branch shoot	with or without shoot
Ecology	Water	Hygrophilous, Tolerant, Xerophilous
	Light	Light, Shadow, Tolerant
	PH	Basic, Neutral, Acide, Tolerant
	Nutriments	Eutrophic, Mesotrophic, Oligotrophic

Gymnosperm species presented generally higher relative abundances than Angiosperm species.

**2.2. Functional traits**

We considered four types of functional diversity, using three main groups of traits: (i) FDr based on reproduction, pollination, bloom, fructification and dispersal traits, (ii) FDM based on morphological

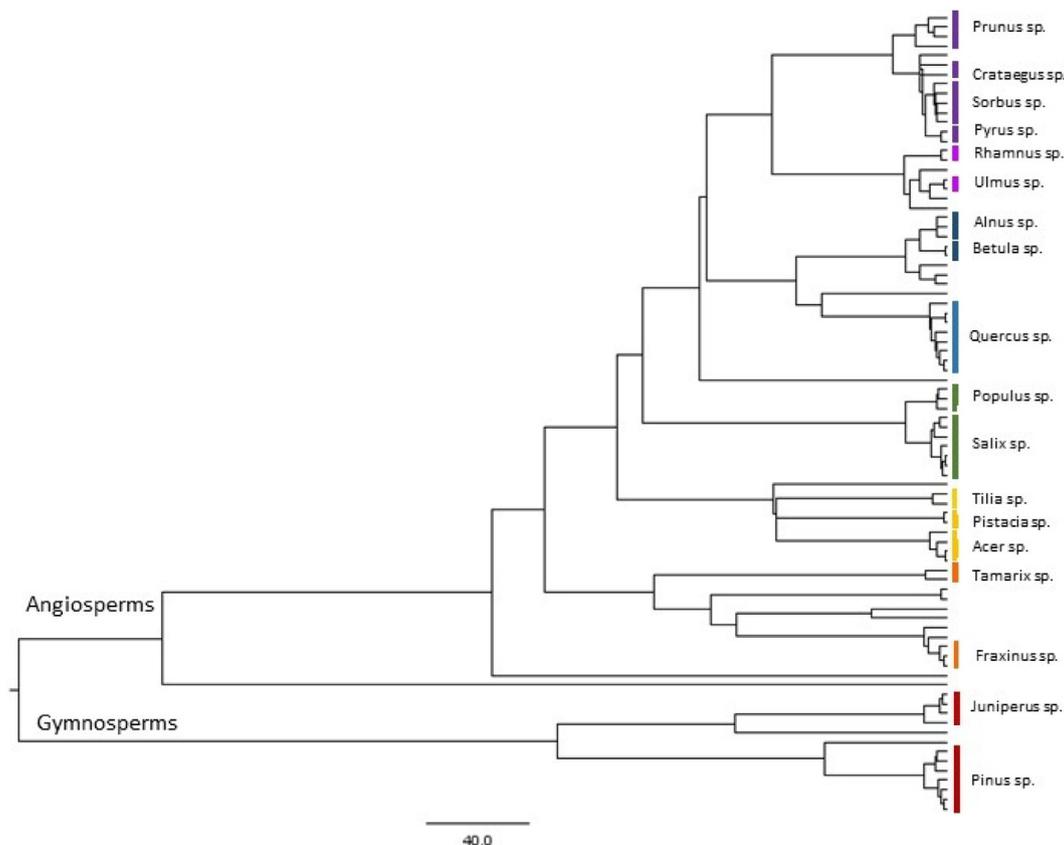
characteristics, like shape and lifespan of leaves, thorniness and trees height, (iii) FDe based on species ecological properties regarding water, soil, light and pH, and finally (iv) FDt was estimated combining all traits together; see Table 1 for traits and modalities.

Functional traits influence ecosystem properties and/or species' responses to environmental conditions and interspecific competition (Grime, 2006). Regeneration traits are plants characteristics that define seed production, seed dispersal, sexuality and phenology, each of which has the ability to influence plant population and community dynamics (Grubb, 1977). Morphological traits correspond to the characteristics of plants shape and structure that have implications in common functions such as intercepting light, fixing carbon and regulating water balance. Ecological modalities correspond to plants ecological preferences regarding water availability, light and soil and although not strictly considered as traits but more as properties (Violle et al., 2007), they are often used to identify species functional role (Ellenberg's indicators for instance; Hill et al., 2000; Diekmann, 2003) and were thus considered in our analysis.

To estimate functional distances among species, we first estimated Gower's distances on traits values, then conducted a principal coordinate analysis (PCoA). We finally retained four principal coordinates for the total FDt, and two for FDr, FDM and FDe. Finally, the Euclidean functional distances were estimated based on the retained coordinates (for more details on the PCoA see Appendix 2).

**2.3. Phylogenetic data**

A molecular phylogeny of the 83 species was constructed using nucleotidic sequence data, available in GenBank. We identified three genes i.e. rbcL, matK and 5.8 s sequences for which there was available information for most of the species considered. The ultrametric phylogenetic tree was obtained by a heuristic search of a maximum



**Fig. 1.** Ultrametric phylogenetic tree of 83 French Mediterranean tree species, based on a concatenation of rbcL, matK and 5.8 s sequences. The main genera are indicated in the tips of the tree (for detailed information per species see Appendix 3).

parsimony analysis (for more details see Appendix 3). After corrections for missing molecular data using TreeGraph2 software (Stöver & Müller, 2010), the final tree was converted to an ultrametric tree with the ape R package (Paradis et al., 2019). The phylogenetic tree was composed principally by angiosperms ( $N = 70$ ) and in a much less extent by gymnosperm species ( $N = 13$ ) (Fig. 1). Phylogenetic distance was estimated as the distance between a set of tips of the phylogeny.

We analyzed the phylogenetic signal present in the functional traits matrix. As the trait dataset is composed by discrete variables, we used a multiple correspondence analysis (MCA of ade4 R package) to identify principal axes and then used them as continuous variables to estimate phylogenetic conservatism, i.e. the tendency of phylogenetically related species to be functionally similar. We used the phyloSignal R package (Keck et al., 2016), as it implements several indices of phylogenetic signal, as well as phylogenetic autocorrelation analyses. Further details are given in the Appendix 4.

#### 2.4. Taxonomic, functional and phylogenetic tree diversity

We used the quadratic entropy Rao index to estimate all three diversity facets i.e. TD, FD and PD (Pavoine et al., 2004; Ricotta, 2005; De Bello et al., 2010). The diversity of each community is estimated by the equation:

$$Q = \sum_{i=1}^S \sum_{j=1}^S d_{ij} p_i p_j, \quad (1)$$

where  $p_i$  and  $p_j$  are the frequencies of species  $i$  and  $j$  and  $d_{ij}$  is the distance between them. In our case, relative abundance ( $p$ ) was the estimate of the relative coverage of each taxa per plot, as recorded by the IGN. For TD,  $d_{ij}$  was set to 1 for all species pairs, resulting to the Simpson diversity index (Ricotta, 2005). For FD,  $d_{ij}$  was estimated as the corresponding Euclidean distance, as resulted from the PCoA, after scaling values between 0 and 1, by dividing by their maximum. For PD,  $d_{ij}$  was replaced by the ultrametric phylogenetic distances between species and then divided by their maximum, to obtain distances with range from 0 to 1. Thus for FD and PD,  $d_{ij}$  equals 0, indicates the distance between individuals of the same species and  $d_{ij}$  equals 1 indicates the distance between the most distinct (functionally or phylogenetically) species.

To test whether the observed trends and congruence reflect ecological processes or are simply due to correlations observed by sampling effects, we used a null modelling approach. For each plot, we kept the species number and their relative abundances unchanged and only randomly shifted the species names by others among the study species pool. This randomisation keeps the taxonomic diversity unchanged for random values of FD and PD (Hardy, 2008; Calba et al., 2014). We repeated this random sampling procedure 1000 times for each of the diversity indices. We then estimated the standardised effect size (SES), following the equation:

$$SES = \frac{Div_{obs} - \bar{Div}_{sim}}{sd_{sim}}, \quad (2)$$

where  $Div_{obs}$  is the observed diversity value,  $\bar{Div}_{sim}$  is the mean simulated diversity value and  $sd_{sim}$  is the standard deviation of the simulated diversity values. The SES approach is commonly used in multifaceted diversity analyses (Mori et al., 2015; Liu et al., 2016). Negative SES values indicate that the observed diversity values are lower than expected, indicating that the assemblages are composed by species with more similar traits and/or by more phylogenetically close species than random (functional and/or phylogenetic clustering) (De Bello et al., 2009; Cavender-Bares et al., 2009). Positive SES values indicate that the observed values result higher than the simulated ones, which indicates a phylogenetic and/or traits divergence within communities (De Bello et al., 2009; De Bello et al., 2012). The maps were produced using automatic kriging models (Hiemstra et al., 2010) through R (package

automap) (R Development Core Team, 2014). We used interpolation only to produce maps, i.e. only for visual representation of diversities spatial distribution, but all further analysis was conducted on the diversities per plot.

#### 2.5. Spatial (auto)correlation patterns among diversity facets

We defined the distance until which the spatial autocorrelation effect is present by using simultaneous autoregressive (SAR) models. These models extend standard linear models by using a spatial autocorrelation component, defined by the neighbourhood weights and the distance until which neighbours are considered (Kissling & Carl, 2008). We tested several neighbourhood distances, from 20 to 150 km, in 10-km intervals for the first 100 km and in a 50-km interval until 150 km. The neighbourhood weights were then defined as  $1/x^2$ , where  $x$  equals each considered distance, which results in attributing higher weights to closer neighbours. The best spatial model was chosen based on the lowest AIC value (Kissling & Carl, 2008; Meynard et al., 2013). We further verified the models residuals for any remaining spatial autocorrelation pattern using the Moran's  $I$  index through correlograms (Legendre & Fortin, 1989). If a spatial correlation pattern is present, the Moran's  $I$  index will be relatively high at small distance intervals and will get negative values as distance progressively increases (Legendre & Fortin, 1989).

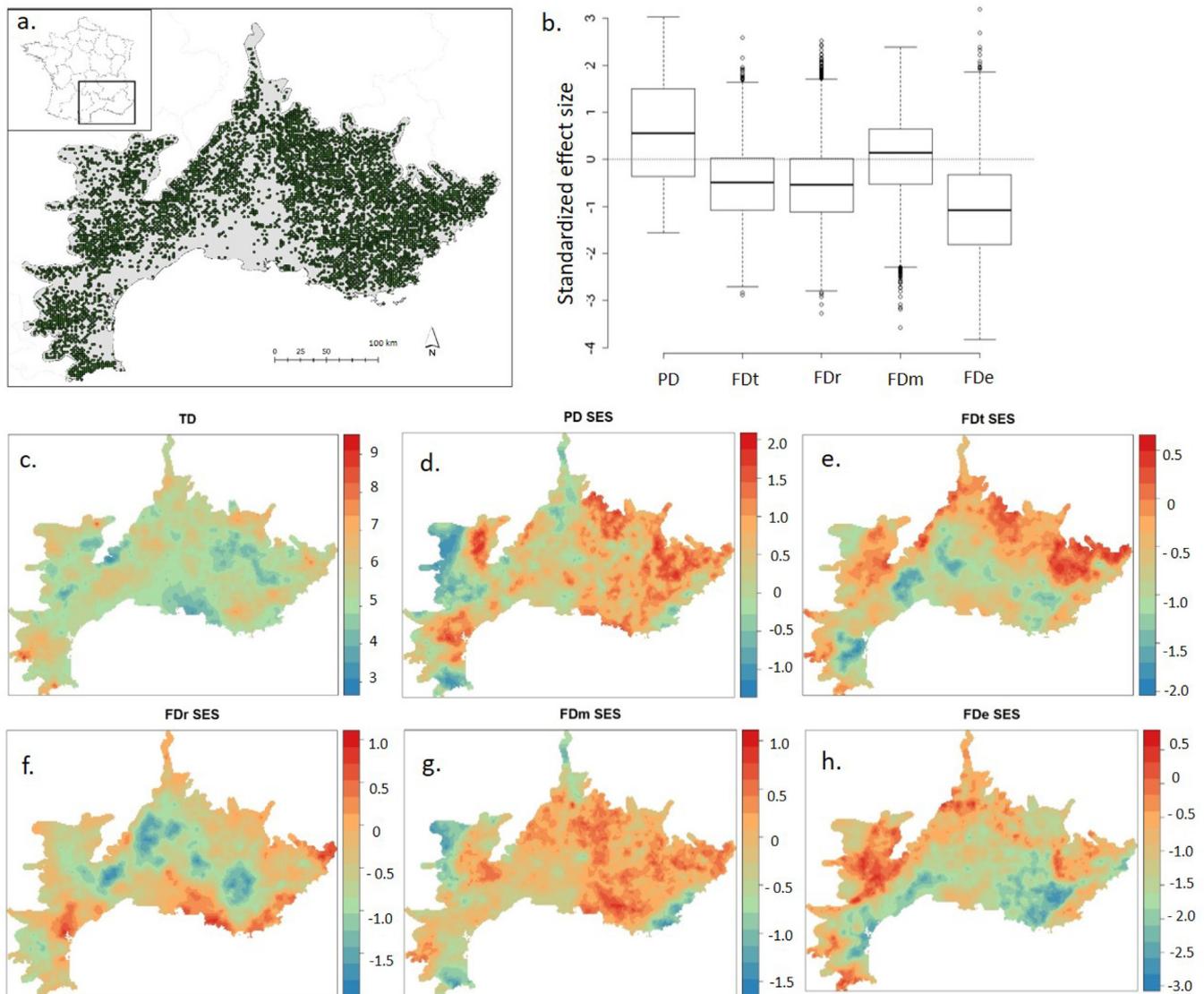
We further used the retained SAR model per diversity facet to estimate the relationships - slope and standard error - between PD and the FD types. We finally compared these results with a commonly used approach in spatial autocorrelation analysis, by conducting the partial Mantel tests. These tests allow to calculate the spatial correlations between two distance matrices (in our case PD and FD), conditioned by a third matrix corresponding to geographical distances between communities (Legendre & Legendre, 2012). The Euclidean distance measures are used for the matrices. Partial Mantel tests ranged from 0, i.e. non-correlated, to 1, i.e. completely correlated diversity indices. The significance of the partial Mantel tests was defined by conducting 1000 iterations.

All statistical analyses and plots were produced using packages base, stats, ncf and vegan in R (3.1.0) (R Development Core Team, 2014).

### 3. Results

We obtained different spatial distributions for TD, FD and PD and FD spatial patterns differed according to the type of traits considered. The SES values for the functional diversity indices were mostly negative, suggesting that species composing the observed assemblages tended to have more similar traits than randomly expected, given the regional species pool, especially for the total FDT and for FDR and FDE indices (Fig. 2b, e, f and h). For the FDM, SES values were mostly around zero, indicating neither traits convergence nor divergence compared to random (Fig. 2b and g). On the contrary, PD SES values were mostly higher than random, indicating that observed species were more phylogenetically distinct than random assemblages (Fig. 2b and d). Our hypothesis was that this result was due to the Angiosperm/Gymnosperm contrast in abundances and phylogeny within communities. Indeed, by excluding Gymnosperms from our species pool, the PD values were lower, mostly around zero (Appendix 5). Comparing the spatial distributions of the diversity facets, different high diversity areas were identified according to the diversity indices and the traits considered (Fig. 2c-h). High FDR areas were mainly observed in the southern part of the Mediterranean France, whereas FDE rich communities were localised mainly in the northern part of our study area. PD values were relatively high over a large part of the study area.

The analysis of phylogenetic signal revealed the presence of traits conservatism, however this concerned specific taxa such as Tamarix sp., Acer sp., Salix sp., Populus sp., Juniperus sp. and Pinus sp., whereas other large clades show non-significant or low phylogenetic signal (see



**Fig. 2.** a. Study area and spatial distribution of the relevés plots, indicated by green spots. The unsampled areas correspond to non forest areas according to the French National Forest Inventory. b. The standardised effect size for phylogenetic (PD), functional diversity based on all traits (FDt), FD based on regeneration traits (FDr), FD based on morphology traits (FDM), and FD based on ecological properties (FDe). Boxplots indicate minimum, 1st quartile, median, 3rd quartile and maximum values per facet. c–h. Spatial distribution of taxonomic diversity (TD), phylogenetic standardised effect size (PD SES), functional standardised effect size (FDt SES), and the three functional diversity indices: FDr SES, FDM SES and FDe SES. Colour intensity indicate increasing values for each diversity indicator. Positive (and respectively negative) values indicate that the observed diversity facets are higher (and respectively lower) than expected in random, given the regional species pool. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Appendix 4, Fig. A4c).

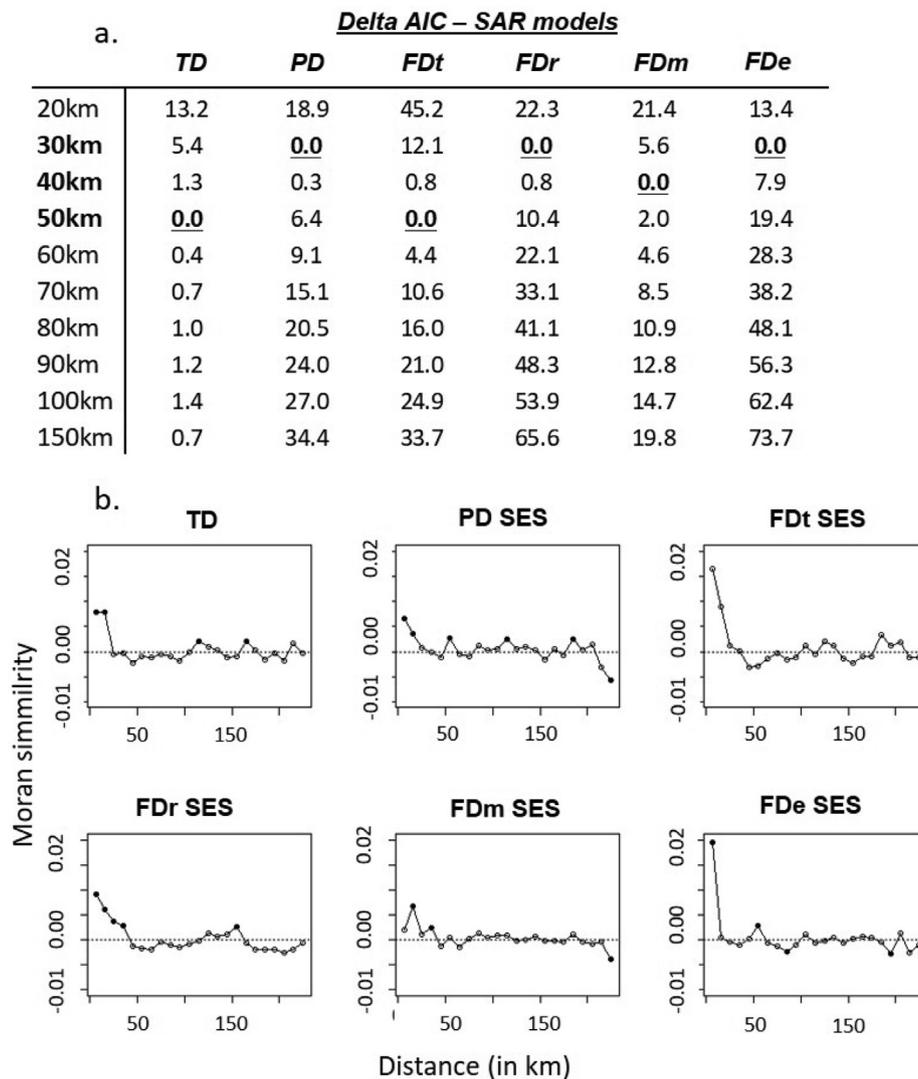
Spatial autocorrelation patterns were revealed for all diversity indices. The lowest AIC values of the SAR spatial models were obtained in a distance of 30 km for PD, FDr and FDe, in 40-km distance for FDM and in 50-km neighbourhood distance for TD and FDt (Fig. 3a). No remaining spatial autocorrelation pattern was observed in the residuals of the diversity indices, after including the corresponding spatial component and Moran similarity  $I$  values were null ( $< 0.02$  in all cases) (Fig. 3b).

Including the autocorrelation pattern identified per facet, SAR models revealed that the PD was only slightly positively linked to FDt (slope = 0.13, se = 0.01) and to FDr (slope = 0.12, se = 0.01). Stronger slope was obtained for PD and FDM (slope = 0.32, se = 0.01); PD was negatively linked to FDe (slope = -0.28, se = 0.01; Fig. 4). The partial Mantel tests showed very low spatial correlation patterns between the PD and FDt ( $r = 0.03$ ,  $p = 0.001$ ), as well as between PD and FDe ( $r = 0.06$ ,  $p = 0.001$ ), while no significant correlation was

revealed between PD and FDr ( $p = 1$ ). The highest spatial correlation was obtained between PD and FDM ( $r = 0.19$ ,  $p = 0.001$ ).

#### 4. Discussion

We used a large number of traits to increase our ability to detect functional differences among the Mediterranean tree species communities (Petchev and Gaston, 2002; Cadotte et al., 2011) and to be able to broadly investigate FD and PD relationships. We selected commonly used traits, which are connected to basic plant functions, like dispersal and regeneration strategy, interception of light resources, water balance and resistance to disturbance (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). However, several of these functions may be connected simultaneously to various ecosystemic mechanisms or processes. For instance, species responses to drought or fire, can be reflected by both regeneration and morphology traits. On the other hand, species that share similar preferences in terms of water and light, may



**Fig. 3.** a. The delta AIC of the simultaneous autoregressive (SAR) models for various neighbour distances from 20 to 150 km. b. The correlograms of the residuals of the SAR models were obtained for neighbour distances set to 30 km for PD SES, FDr SES and FDe SES, to 40 km for FDm SES and to 50 km for TD and FDt SES. Significant Moran's  $I$  values ( $p < 0.05$ ) are shown in black dots and non-significant values ( $p > 0.05$ ) in white dots.

have different morphological traits. Xerophilous species for instance, have various leaf types, like sclerophyllous, acicular and scale shapes, but can all respond similarly to low water availability. Thus, in areas with high functional diversity of morphological traits, functional diversity of ecological properties may be low. This may explain the mismatches we revealed in the spatial structure of diversity facets for the Mediterranean trees in southern France.

Regardless the type of traits, phylogenetic diversity was generally only weakly correlated to functional diversity. A phylogenetic signal was revealed in functional traits, i.e. the tendency of phylogenetically related species to be functionally similar. However, it was only due to certain clades of the phylogenetic tree i.e. the Gymnosperms, the Malpighiales, Caryophyllales and Ericales. The species that compose a given community as well as their relative abundances result from a number of biotic and abiotic factors (Lebrija-Trejos et al., 2010). As a result diversity estimates also depend on composition and evenness factors within communities (De Bello et al., 2009). Overall, the phylogenetic signal in traits was insufficient to cause a high correlation between FD and PD indices in this study.

We also revealed that the phylogenetic diversity was mostly higher than expected by random, given the regional species pool, indicating a phylogenetic divergence, whereas the four functional diversity types

were mostly lower than randomly expected, indicating traits convergence (De Bello et al., 2009). Especially, FD based on water, light availability, pH and soil nutrients properties, was considerably lower than expected, indicating that species environmental properties are more similar among trees assemblages than what one would expect given the regional species pool. Competing mechanisms may act on trees assemblages' composition, with climate and fire potentially driving convergence in traits and resulting to functional and phylogenetic clustering in plants (Verdú & Pausas, 2007; Nóbrega et al., 2019), while biotic factors, like competitive exclusion through species niche overlap, may force species to select different adaptations in order to remain competitive and thus cause traits divergence (Webb et al., 2010; Cadotte et al., 2011). In which direction and what extent these abiotic or biotic filters drive the observed mismatches in FD and PD should be further analyzed.

Whether FD and PD facets indicate functional and phylogenetic convergence or divergence largely depend on the variation of traits and phylogenetic distances encountered within the Mediterranean regional species pool (Calba et al., 2014). This is nicely illustrated, in our case, by examining the structure of the phylogenetic tree. The highest phylogenetic distances were observed within assemblages that were composed both by angiosperm and gymnosperm species. Within the species

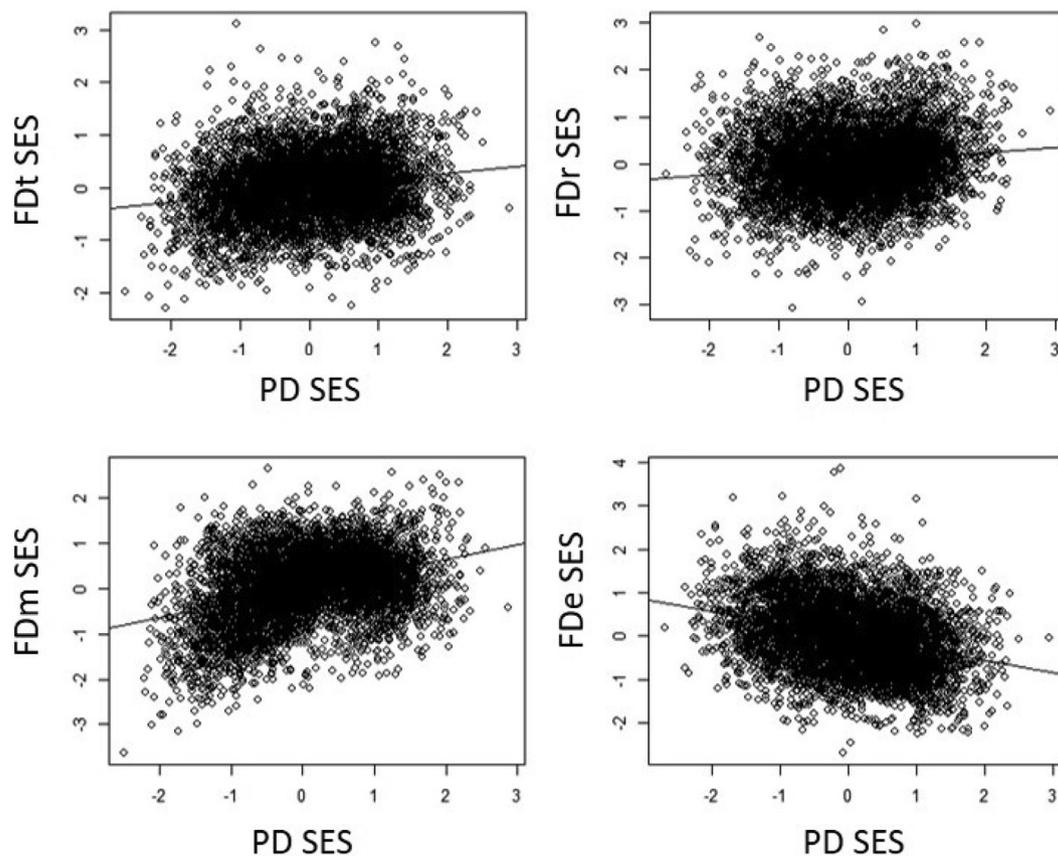


Fig. 4. Relationships between PD SES and the four FD types, FDt SES, FDr SES, FDM SES and FDe SES. These relationships resulted from the SAR models, including the corresponding neighbour distance per diversity facet.

pool, gymnosperms were considerably outnumbered (13 out of 83) but still overrepresented in terms of relative abundances within the Mediterranean region. This mainly concerned *Juniperus* and *Pinus* genera, composed by typical Mediterranean tree species. Given that the Rao index is based on species relative abundances, the presence of few but abundant gymnosperm species within the assemblage automatically increases the observed PD. Yet, when conducting randomisation processes, the probability of replacing a gymnosperm species by an angiosperm one is considerably high, which may explain why the observed phylogenetic diversity values were higher than the random ones (present study). On the other hand, gymnosperm and angiosperm tree species may share similar morphological adaptations in leaf traits for instance, so altering a gymnosperm by an angiosperm tree species during randomisation process was not reflected in our case in the assemblages' functional diversity.

Several biogeographic, environmental but also anthropogenic factors have influenced the Mediterranean landscape and determined the tree species distributions (Quézel & Médail, 2003; Blondel, 2006; Ali et al., 2019). Following agricultural abandonment over the past half a century, for instance, reforestation took place in several places in the Mediterranean region (Serra et al., 2008). Species respond differently and with different paces to spatio-temporal changes in land-use, or even following fires (Baeza et al., 2011; Nóbrega et al., 2019), resulting to different diversity facets distributions. Typically, taxonomic diversity can be high in areas of recent land-use modifications, while the functional and phylogenetic diversity will be low (Purschke et al., 2013). Moreover, the loss in phylogenetic and functional diversity facets may be considerably higher, for instance in case of fire, than the one observed in terms of taxonomic diversity (Nóbrega et al., 2019) and thus using only taxonomic diversity indices may be misleading to properly estimate the impacts of natural and anthropogenic factors on tree

assemblages.

#### 4.1. Spatial congruence and conservation implications

The use of a single facet as a surrogate for the others can be misleading for Mediterranean woody plant assemblages and future conservation hotspots should be defined using complementary diversity facets (Devictor et al., 2010; Mazel et al., 2014). We suggest that functional trait approaches should mainly focus on traits that enable to isolate specific ecosystem functions, mechanisms and/or processes, such as fire regimes or land-use changes, for which species may develop different responses (Elmqvist et al., 2003; Mori et al., 2013).

In this study we used fine scale data (at 1 km resolution), because we wanted to examine the spatial autocorrelation patterns of the diversity indices. Based on our analysis, spatial autocorrelation patterns were present in all diversity indices mainly within a distance of 30 to 50 km. Apart from the statistical importance of handling spatial autocorrelation, our particular interest was to determine an adequate scale at which one may study tree diversity distribution patterns. Especially when dealing with large scale analyses, at the global scale or when including data from different biomes for instance, fine resolution data are difficult or even impossible to gather. On the other hand, pooling or using data at a coarse scale may in some cases disregard the variance within diversity patterns. Indeed, local scale processes acting on communities' assembly processes may be neglected when considering large spatial scales. We propose that a 30 to 50 km resolution is an adapted resolution for spatial analyses of tree assemblages' diversity facets, which is consistent with previous work on large scale tree species richness (Montoya et al., 2007).

Analysing multifaceted diversity distributions at adequate resolutions and scales is also important in order to be able to identify species

refugia and provide more accurate estimations about their link to environmental variables, such as elevation-related factors, and/or to current and future risks, like changes in climate and fire regimes. Elevation-related environmental conditions may be reflected on the spatial distribution of diversity facets and might explain their mismatches, yet acting at different scales. Fine resolution variables for instance, such as topographic slopes and sun radiation may be related to fine resolution TD, FD and PD patterns, while climatic variables, like temperature and precipitation rates, might be linked to diversity facet patterns at coarser resolutions. Spatial variation and structure coming from fine resolution diversity maps, such as the ones provided here, may help reducing the risk of ignoring macro or even micro refugia for conservation purposes that, given their climatic and geomorphological specificities, may continue to be an important component of landscape diversity even if the composition of species changes (Hamrick, 2004; Mosblech et al., 2011).

Further analyses between the functional, phylogenetic and taxonomic diversity and the climatic refugia could help identify the spatial connection among them and offer new conservation perspectives at the regional level (Mosblech et al., 2011; Stewart et al., 2010; Hampe et al., 2013). Moreover, future analyses should bring light to the exact anthropogenic and natural factors that may have shaped these distributions and may explain the differences we observed in tree diversity facets in the Mediterranean France. Moreover, we revealed some limited similarities between the spatial patterns of phylogenetic and functional diversity based on morphological traits that might indicate a common environmental driver, as for example, the elevation gradient (Chun & Lee, 2017). It would thus be interesting to test this hypothesis over a large spatial extent (ex. the entire Mediterranean biome) to better capture environmental variability and investigate whether high phylogenetic (and/or functional) diversity occurs for instance in high or in intermediate elevation levels (Zhu et al., 2019), which could also permit testing hypotheses between woody plant diversity facets and the climatic refugia.

This study showed that all three diversity facets give complementary information about the tree biodiversity hotspots in the French Mediterranean region. Complexity in species responses and tree diversity indices should be explained by the complex biogeography and high climatic and topographic heterogeneity in the Mediterranean region (Médail et al., 2019; Doxa & Prastacos, 2020). With the use of prioritisation algorithms, the biodiversity facets may be used as input to provide conservation planning scenarios under past, present or future environmental conditions (Doxa et al., 2017; Marignani et al., 2017). However, it is important to note that describing several biodiversity facets is not in itself sufficient to define optimal conservation strategies. Depending on the ecological trajectory of a given area, TD, FD and PD can be low and yet correspond to places of major conservation importance. Moreover, even though biodiversity is expected to be higher in natural woodlands, even in monospecific tree assemblages, herbaceous plant diversity may be considerably high, also leading to high diversity levels for insects, birds and mammals (da Silva et al., 2019). Here we focused on a specific geo-climatic zone and vegetation type considering only tree species. Future research will be needed to investigate whether diversity facets are linked to land-use and climate changes over the Mediterranean biome.

#### CRedit authorship contribution statement

**Aggeliki Doxa:** Conceptualization, Methodology, Formal analysis, Writing - original draft. **Vincent Devictor:** Conceptualization, Methodology, Writing - review & editing. **Alex Baumel:** Methodology, Formal analysis, Writing - review & editing. **Daniel Pavon:** Resources. **Frédéric Médail:** Conceptualization, Writing - review & editing, Supervision. **Agathe Leriche:** Conceptualization, Methodology, Writing - review & editing, Supervision.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Acknowledgements

This study was funded by Aix Marseille University as a F2IR post-doctoral grant. We thank all those that worked in the field to collect the data and the National Forest Inventory (IGN) for providing these data. We also thank Virgile Noble for his helpful advice and comments during the early conception stage of this work.

#### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118318>.

#### References

- Ali, A., Chen, H.Y.H., You, W.H., Yan, E.R., 2019. Multiple abiotic and biotic drivers of aboveground biomass shift with forest stratum. *For. Ecol. Manage.* 436, 1–10.
- Baeza, M.J., Santana, V.M., Pausas, J.G., Vallejo, V.R., 2011. Successional trends in standing dead biomass in Mediterranean basin species. *J. Veg. Sci.* 22, 467–474.
- De Bello, F., Lavergne, S., Meynard, C.N., Lepš, J., Thuiller, W., 2010. The partitioning of diversity: showing Theuse a way out of the labyrinth. *J. Veg. Sci.* 21, 992–1000.
- De Bello, F., Price, J.N., Munkemüller, T., Liira, J., Zobel, M., Thuiller, W., Gerhold, P., Götzberger, L., Lavergne, S., Lepš, J., Zobel, K., Partel, M., 2012. Functional species pool framework to test for biotic effects on community assembly. *Ecology* 93, 2263–2273.
- De Bello, F., Thuiller, W., Lepš, J., Choler, P., Clement, J.C., Macek, P., Sebastia, M.T., Lavorel, S., 2009. Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *J. Veg. Sci.* 20, 475–486.
- Bernard-Verdier, M., Flores, O., Navas, M.L., Garnier, E., 2013. Partitioning phylogenetic and functional diversity into alpha and beta components along an environmental gradient in a Mediterranean rangeland. *J. Veg. Sci.* 24, 877–889.
- Blondel, J., 2006. The “design” of Mediterranean landscapes: a millennial story of humans and ecological systems during the historic period. *Hum. Ecol.* 34, 713–729.
- Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S.L., 2006. Global biodiversity conservation priorities. *Science (New York, N.Y.)* 313, 58–61.
- Cadotte, M.W., Cardinale, B.J., Oakley, T.H., 2008. Evolutionary history and the effect of biodiversity on plant productivity. *Proc. Natl. Acad. Sci. U.S.A.* 105, 17012–17017.
- Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48, 1079–1087.
- Calba, S., Maris, V., Devictor, V., 2014. Measuring and explaining large-scale distribution of functional and phylogenetic diversity in birds: separating ecological drivers from methodological choices. *Glob. Ecol. Biogeogr.* 23, 669–678.
- Carboni, M., Acosta, A.T.R., Ricotta, C., 2013. Are differences in functional diversity among plant communities on Mediterranean coastal dunes driven by their phylogenetic history? *J. Veg. Sci.* 24, 932–941.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. *Ecol. Lett.* 12, 693–715.
- Chun, J.H., Lee, C.B., 2017. Disentangling the local-scale drivers of taxonomic, phylogenetic and functional diversity in woody plant assemblages along elevational gradients in South Korea. *PLoS ONE* 12, e0185763.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H., Morgan, H.D., Van Der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51, 335–380.
- Devictor, V., Moullot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.* 13, 1030–1040.
- Diekmann, M., 2003. Basic and Applied Ecology Species indicator values as an important tool in applied plant ecology – a review. *Basic Appl. Ecol.* 4, 493–506.
- Doxa, A., Albert, C.H., Leriche, A., Saatkamp, A., 2017. Prioritizing conservation areas for coastal plant diversity under increasing urbanization. *J. Environ. Manage.* 201, 425–434.
- Doxa, A., Prastacos, P., 2020. Using Rao’s quadratic entropy to define environmental heterogeneity priority areas in the European Mediterranean biome. *Biol. Conserv.* <https://doi.org/10.1016/j.biocon.2019.108366>.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change and resilience. *Front. Ecol. Environ.* 1, 488–494.
- Fady, B., Conord, C., 2010. Macroecological patterns of species and genetic diversity in vascular plants of the Mediterranean basin. *Divers. Distrib.* 16, 53–64.

- Gerhold Jr., P., Cahill, J.F., Winter, M., Bartish, I.V., Prinzing, A., 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Funct. Ecol.* 29, 600–614.
- Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *J. Veg. Sci.* 17, 255–260.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of regeneration niche. *Biol. Rev.* <https://doi.org/10.1111/j.1469-185x.1977.tb01347.x>.
- Hampe, A., Rodriguez-Sanchez, F., Dobrowski, S., Hu, F., Gavin, D., 2013. Climate refugia: from the Last Glacial maximum to the twenty first century. *New Phytol.* 197, 16–18.
- Hamrick, J.L., 2004. Response of forest trees to global environmental changes. *For. Ecol. Manage.* 197, 323–335.
- Hao, M., Ganeshaiah, K.N., Zhang, C., Zhao, X., von Gadow, K., 2019. Discriminating among forest communities based on taxonomic, phylogenetic and trait distances. *For. Ecol. Manage.* 440, 40–47.
- Hardy, O.J., 2008. Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *J. Ecol.* 96, 914–926.
- Hiemstra, P.H., Pebesma, E.J., Heuvelink, G.B.M., Twenhofel, C.J.W., 2010. Using rainfall radar data to improve interpolated maps of dose rate in the Netherlands. *Sci. Total Environ.* 409, 123–133.
- Hill, M.O., Roy, D.B., Mountford, J.O., Bunce, R.G.H., 2000. Extending Ellenberg's indicator values to a new area: an algorithmic approach. *J. Appl. Ecol.* 37, 3–15.
- Keck, F., Rimet, F., Bouchez, A., Franc, A., 2016. Phylsignal: an R package to measure, test, and explore the phylogenetic signal. *Ecol. Evol.* <https://doi.org/10.1002/ece3.2051>.
- Kissling, W.D., Carl, G., 2008. Spatial autocorrelation and the selection of simultaneous autoregressive models. *Glob. Ecol. Biogeogr.* 17, 59–71.
- Laughlin, D.C., 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. *J. Ecol.* 102, 186–193.
- Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F., Poorter, L., 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* 91, 386–398.
- Legendre, P., Fortin, M.J., 1989. Spatial pattern and ecological analysis. *Plant Ecol.* 80, 107–138.
- Legendre, P., Legendre, L., 2012. Complex ecological data sets. *Numer. Ecol. (Develop. Environ. Model.)* 1–57.
- Liu, C., Guenard, B., Blanchard, B., Peng, Y., Economo, E.P., 2016. Reorganization of taxonomic, functional and phylogenetic ant biodiversity after conversion to rubber plantation. *Ecol. Monogr.* 86, 215–227.
- Marignani, M., Bruschi, D., Astiaso Garcia, D., Frondoni, R., Carli, E., Pinna, M.S., Cumo, F., Gugliermetti, F., Saatkamp, A., Doxa, A., Queller, E.M., Chaieb, M., Bou Dagher-Kharrat, M., El Zein, R., El Jeitani, S., Khater, C., Mansour, S., Al-Shami, A., Harik, G., Alameddine, I., El-Fadel, M., Blasi, C., 2017. Identification and prioritization of areas with high environmental risk in Mediterranean coastal areas: a flexible approach. *Sci. Total Environ.* 590–591, 566–578.
- Mason, N.W.H., Pavoine, S., 2013. Does trait conservatism guarantee that indicators of phylogenetic community structure will reveal niche-based assembly processes along stress gradients? *J. Veg. Sci.* 24, 820–833.
- Mazel, F., Guilhaumon, F., Mouquet, N., Devictor, V., Gravel, D., Renaud, J., Cianciaruso, M.V., Loyola, R., Diniz-Filho, J.A.F., Mouillot, D., Thuiller, W., 2014. Multifaceted diversity-area relationships reveal global hotspots of mammalian species, trait and lineage diversity. *Glob. Ecol. Biogeogr.* 23, 836–847.
- Médail, F., Monnet, A.C., Pavan, D., Nikolic, T., Dimopoulos, P., Bacchetta, G., Arroyo, J., Barina, Z., Albassatneh, M.C., Domina, G., Fady, B., Matevski, V., Mifsud, S., Leriche, A., 2019. What is a tree in the mediterranean basin hotspot? A critical analysis. *Forest Ecosyst.* <https://doi.org/10.1186/s40663-019-0170-6>.
- Meynard, C.N., Boulangeat, I., Garraud, L., Mouquet, N., Thuiller, W., 2013. Disentangling the drivers of metacommunity structure across spatial scales. *J. Biogeogr.* 40, 1560–1571.
- Meynard, C.N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F., Mouquet, N., 2011. Beyond taxonomic diversity patterns: How do  $\alpha$ ,  $\beta$  and  $\gamma$  components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Glob. Ecol. Biogeogr.* 20, 893–903.
- Montoya, D., Rodríguez, M.A., Zavala, M.A., Hawkins, B.A., 2007. Contemporary richness of holarctic trees and the historical pattern of glacial retreat. *Ecography* 30, 173–182.
- Mori, A.S., Furukawa, T., Sasaki, T., 2013. Response diversity determines the resilience of ecosystems to environmental change. *Biol. Rev.* 88, 349–364.
- Mori, A.S., Ota, A.T., Fujii, S., Seino, T., 2015. Biotic homogenization and differentiation of soil faunal communities in the production forest landscape: taxonomic and functional perspectives. *Oecologia* 177, 533–544.
- Mosblech, N.A.S., Bush, M.B., Van Woesik, R., 2011. On metapopulations and micro-refugia: Palaeoecological insights. *J. Biogeogr.* 38, 419–429.
- Mouillot, D., Albouy, C., Guilhaumon, F., Ben Rais Lasram, F., Coll, M., Devictor, V., Meynard, C.N., Pauly, D., Tomasini, J.A., Troussellier, M., Velez, L., Watson, R., Douzery, E.J.P., Mouquet, N., 2011. Protected and threatened components of fish biodiversity in the Mediterranean sea. *Curr. Biol.* 21, 1044–1050.
- Mouquet, N., Devictor, V., Meynard, C.N., Munoz, F., Bersier, L.-F., Chave, J., Couteron, P., Dalecky, A., Fontaine, C., Gravel, D., Hardy, O.J., Jabot, F., Lavergne, S., Leibold, M., Mouillot, D., Münkemüller, T., Pavoine, S., Prinzing, A., Rodrigues, A.S.L., Rohr, R.P., Thébault, E., Thuiller, W., 2012. Ecophylogenetics: advances and perspectives. *Biol. Rev. Camb. Philos. Soc.* 87, 769–785.
- Nóbrega, C.C., Brando, P.M., Silvério, D.V., Maracahipes, L., de Marco, P., 2019. Effects of experimental fires on the phylogenetic and functional diversity of woody species in a neotropical forest. *For. Ecol. Manage.* 450, 117497.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., et al., 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* 51, 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:teotwa\]2.0.co;2](https://doi.org/10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2).
- Pagel, M., 1999. Inferring the historical patterns of biological evolution. *Nature* 401, 877–884.
- Paradis, Emmanuel, Schliep, Klaus, Schwartz, Russell, 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35 (3), 526–528. <https://doi.org/10.1093/bioinformatics/bty633>.
- Pavoine, S., Dufour, A.B., Chessel, D., 2004. From dissimilarities among species to dissimilarities among communities: a double principal coordinate analysis. *J. Theor. Biol.* 228, 523–537.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., Vos, A.C. De, Buchmann, N., Funes, G., Hodgson, J.G., Thompson, K., Morgan, H.D., Steege, H., Heijden, M.G.A. Van, Sack Der, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234.
- Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. *Ecol. Lett.* 5, 402–411. <https://doi.org/10.1046/j.1461-0248.2002.00339.x>.
- Purschke, O., Schmid, B.C., Sykes, M.T., Poschlod, P., Michalski, S.G., Durka, W., Kühn, I., Winter, M., Prentice, H.C., 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: Insights into assembly processes. *J. Ecol.* 101, 857–866.
- Quézel, P., Médail, F., 2003. *Ecologie et biogéographie des forêts du bassin méditerranéen*. Elsevier, Paris.
- R Development Core Team, 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing Vienna Austria 0: {ISBN} 3-900051-07-0.
- Ricotta, C., 2005. Additive partitioning of Rao's quadratic diversity: a hierarchical approach. *Ecol. Model.* 183, 365–371.
- Serra, P., Pons, X., Saurí, D., 2008. Land-cover and land-use change in a Mediterranean landscape: a spatial analysis of driving forces integrating biophysical and human factors. *Appl. Geogr.* 28, 189–209.
- da Silva, L.P., Heleno, R.H., Costa, J.M., Valente, M., Mata, V.A., Gonçalves, S.C., da Silva, A.A., Alves, J., Ramos, J.A., 2019. Natural woodlands hold more diverse, abundant, and unique biota than novel anthropogenic forests: a multi-group assessment. *Eur. J. Forest Res.* <https://doi.org/10.1007/s10342-019-01183-5>.
- Stewart, J.R., Lister, A.M., Barnes, I., Dalén, L., 2010. Refugia revisited: individualistic responses of species in space and time. *Proc. Biol. Sci.* 277, 661–671. <https://doi.org/10.1098/rspb.2009.1272>.
- Stöver, B.C., Müller, K.F., 2010. TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinform.* 11, 7.
- Swenson, N.G., 2011. The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. *Am. J. Bot.* 98, 472–480.
- Thuiller, W., Guéguen, M., Georges, D., Bonet, R., Chalmandrier, L., Garraud, L., Renaud, J., Roquet, C., Van Es, J., Zimmermann, N.E., Lavergne, S., 2014. Are different facets of plant diversity well protected against climate and land cover changes? A test study in the French Alps. *Ecography* 37, 1254–1266.
- Tucker, C.M., Cadotte, M.W., 2013. Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. *Divers. Distrib.* <https://doi.org/10.1111/ddi.12087>.
- Verdú, M., Pausas, J.G., 2007. Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *J. Ecol.* 95, 1316–1323.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional. *Oikos* 882–892.
- Webb, C.O., Ackerly, D.D., McPeck, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33, 475–505.
- Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., LeRoy Poff, N., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecol. Lett.* 13, 267–283.
- Winter, M., Devictor, V., Schweiger, O., 2013. Phylogenetic diversity and nature conservation: where are we? *Trends Ecol. Evol.* 28, 199–204.
- Zhu, Z.X., Nizamani, M.M., Sahu, S.K., Kunasingam, A., Wang, H.F., 2019. Tree abundance, richness, and phylogenetic diversity along an elevation gradient in the tropical forest of Diaolu Mountain in Hainan, China. *Acta Oecologica* 101, 103481.