

# Decoupled functional and phylogenetic diversity provide complementary information about community assembly mechanisms: A case study of Greek forests

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## ABSTRACT

Understanding the mechanisms of community assembly is of great importance to biogeography and ecology. Simultaneous investigation of the functional and phylogenetic facets of diversity has been proposed as a useful approach that allows inferences about such mechanisms. This study applies such an approach to explore diversity and structure within and among the main plant community types of mountainous forests in northern and central Greece. Functional and phylogenetic diversity and structure were measured in 25 community types of broad-leaved deciduous and mountainous coniferous forests. Functional richness and Faith's phylogenetic diversity were used to assess diversity, while mean pairwise functional and phylogenetic distances were used to investigate structure. Relationships between both facets of diversity and structure, as well as community types, were tested using boosted regression trees separately for all vascular plant taxa and taxa occurring in the forest understorey. Phylogenetic diversity was positively correlated with functional diversity, but phylogenetic structure was not a good predictor of functional structure. The understorey dataset revealed non-random structure for more vegetation plots than the dataset with all taxa. Habitat effects, represented by community types, were found to be better predictors of functional structure than phylogenetic structure, highlighting the need to account for habitat variability in studies of community assembly. In our study system, the two diversity facets provide complementary information on the structure of community types since most of the vegetation plots studied were found statistically significantly structured for one diversity facet (functionally clustered or phylogenetically over-dispersed) and random for the other. Our results indicate that functional and phylogenetic measures provide different insights into the mechanisms driving the assembly of the forest community types studied.

## 1. Introduction

The framework of community assembly theory has been widely used in recent decades to understand the structuring of natural communities (Keddy, 1992). To disentangle the processes underlying community assembly, apart from taxonomic diversity, ecologists integrate functional diversity (FD), i.e. the diversity of functional traits in a community (Ricotta, 2005), and phylogenetic diversity (PD), i.e. variation in the evolutionary history of species (Webb et al., 2002).

Phylogenetic and functional diversities have often been used

interchangeably, based on the idea of phylogenetic niche conservatism of traits, which assumes that closely related species are more functionally similar than distant relatives. Although the phylogenetic conservatism of traits is common (Wiens et al., 2010), the magnitude of phylogenetic signal varies among traits (Graham et al., 2012), and some traits nearly lack phylogenetic signal (Losos, 2008). By phylogenetic signal we refer to the actual level of resemblance of a set of related species compared to the corresponding resemblance among randomly selected species drawn from the same phylogenetic tree (Münkemüller et al., 2012). Therefore, more in-depth knowledge of community

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assembly mechanisms can be inferred by investigating the combination of functional and phylogenetic randomness, overdispersion or clustering in a community. Functionally and phylogenetically clustered communities have more similar species than random assemblages of species from the regional species pool, whereas overdispersed communities have more dissimilar species than random assemblages (Cavender-Bares et al., 2009; Webb et al., 2002). Traits are more informative about the link between species and ecological processes, capture recent evolutionary divergence and reflect filtering and competitive effects (Cadotte et al., 2019). In contrast, phylogenies reflect processes operating at larger spatial and temporal scales, such as speciation and past migrations (Cadotte et al., 2019; Cavender-Bares et al., 2009; Kallimanis et al., 2021). Simultaneous use of functional and phylogenetic diversity in community ecology has been proposed for at least three decades (Cornwell and Ackerly, 2009; Diaz et al., 1998; Grandcolas, 1998; Losos, 1996; Wanntorp et al., 1990), and a number of theoretical frameworks have been developed to interpret the observed patterns of the phylogenetic and functional structure of communities and their correlations (Kraft et al., 2007; Kraft and Ackerly, 2010; Prinzing et al., 2008; Webb et al., 2002). Interpretations of observed patterns may partly differ between such theoretical concepts, depending on the specific assumptions and parameters included, with environmental filtering and limiting similarity being the two main processes considered to drive community assembly (Emerson and Gillespie, 2008; Kraft et al., 2007; Kraft and Ackerly, 2010).

Despite the increasing use of patterns of functional and phylogenetic diversity and structure in recent years for inferring the drivers of community assembly across a variety of ecosystems, it has been highlighted that safe deductions can only be made when parameters such as the level of trait conservatism or the number of habitats involved in the community sample have been taken into account (Emerson and Gillespie, 2008; Kraft and Ackerly, 2010). On the one hand, the positive correlation of functional and phylogenetic structure, which also implies high phylogenetic trait conservatism, has been attributed to processes such as competitive exclusion and niche differentiation in case of overdispersion, whereas it supports the concept of habitat filtering in case of clustering (Kraft and Ackerly, 2010). On the other hand, a negative correlation between functional and phylogenetic structure can result from various processes, depending on the level of phylogenetic conservatism of the traits used, such as habitat filtering, speciation or adaptive radiation (Emerson and Gillespie, 2008; Kraft and Ackerly, 2010).

Distinct diversity and structure patterns may also arise among habitats due to different biogeographic history of the pools of species specialized for individual habitats (Fine and Kembel, 2011), suggesting that inferences about community assembly are better made separately for each habitat type. Moreover, distinct patterns can arise in different vertical layers of a forest community (overstorey and understorey) due to different environmental conditions, structural complexity and functional strategies of the plant species they include (Chun and Lee, 2019; Wright, 2002). Specifically, large woody plants and herbaceous plants have different niche characteristics that can lead to different assembly processes in the overstorey and understorey (Chai et al., 2016). Therefore, more accurate conclusions regarding community assembly can be obtained by studying forest layers separately, since environmental filtering mainly affects dominant species in the canopy layer, while niche differentiation is more relevant for species of the herb layer (Chun and Lee, 2019; Maire et al., 2012).

In this case study, we use mountainous forest types of northern and central Greece to investigate the potential correlation or complementarity between phylogenetic and functional diversity and structure patterns at a fine spatial scale. This area is characterized by a large topographic and ecological heterogeneity in just 2 degrees of latitude. Two previous studies have independently explored the patterns of phylogenetic and functional diversity and structure of forest vegetation in this area (Mastrogianni et al., 2019, 2021). Additional investigation of the relationship between the two aspects of diversity can provide a

better understanding of the actual drivers of community assembly in these ecosystems, but also of the potential causes of congruences or incongruences in diversity.

Therefore, the main objectives of the present study were to investigate i) if phylogenetic diversity is a good surrogate of functional diversity for our dataset, ii) if these two diversity metrics are characterized by a congruent or incongruent pattern among different vegetation layers and iii) if the two diversity metrics are characterized by a congruent or incongruent pattern among the different general forest habitats.

## 2. Methods

### 2.1. Study area and dataset

The study area includes five of the 13 floristic regions of Greece (Strid and Tan, 1997), namely North East, North Central, East Central, North Pindos and South Pindos. While Greece in general has high endemism (Médail and Quézel, 1997), our study area additionally includes three putative refugial areas as proposed by Médail and Diadema (2009), namely Mt. Pindos, Mt. Olympus - Mt. Kato Olympus, and the Chalkidiki region. Evidence of refugia for several species and different forest community types in this area has been provided by pollen records and species genetic diversity (Bennett et al., 1991; Tzedakis et al., 2013).

Our dataset consisted of forest vegetation plots from the study area, mainly derived from two vegetation-plot databases of Greek forests (EU-GR-006 Hellenic Woodland Database & EU-GR-007 Hellenic Beech Forests Database; Fotiadis et al., 2012; Tsiripidis et al., 2012). These databases were revised and extended with new sampling (85 plots in ravine forests) and the collection of additional data from the literature. Subsequently, all plots with tree species typical of deciduous broad-leaved and mountainous coniferous forests and with an additive cover of at least 38% (average cover of degree 3 on the Braun-Blanquet scale) were selected, leading to a final dataset of 3493 plots. Species taxonomy and nomenclature were unified according to the Euro + Med PlantBase (Euro + Med, 2006–2021). The plots were classified as described in Mastrogianni et al. (2019). The final classification scheme included 25 ecologically and floristically interpretable community types belonging to four general forest types: beech (nine community types presented here with IDs 1–9), ravine (three community types, 10–12), pine (five community types, 13–17) and oak forests (eight community types, 18–25). See Mastrogianni et al. (2019) for more details on the dataset, the 25 vegetation communities and their ecological and floristic differentiation.

We analysed the dataset considering all the vascular plant taxa present. To account for differences between forest layers, we also analysed a data subset including only non-phanerophyte taxa, representing the understorey vegetation. The complete dataset is hereafter called ALL, whereas the non-phanerophyte subset is called UNDER. Because of a small number of phanerophyte taxa in the ALL dataset, we did not analyse a subset of overstorey vegetation.

### 2.2. Functional and phylogenetic diversity and structure

We used a dataset of 16 functional traits collected from literature sources for 923 vascular plant taxa that were taxonomically identified below the genus level and had at least five occurrences in the 3493 forest plots. The list of the functional traits, the level of data completeness, and the literature sources used are presented in Appendix A. A more detailed description of these traits, the selection process and additional information regarding gap-filling are given in Mastrogianni et al. (2021). The phylogenetic data were extracted from the species-level megaphylogeny of Zanne et al. (2014) updated by Qian and Jin (2016). The phylogenetic tree was constructed with the “S.PhyloMaker” function (Qian and Jin, 2016) in the R package “picante” (Kembel et al., 2010). The taxa missing in the megaphylogeny were randomly distributed among branch tips within their genera, following the proposal of Qian and Jin (2016).

Further details can be found in [Mastrogianni et al. \(2019\)](#).

Functional and phylogenetic diversity and structure indices were estimated at the plot level. We selected the indices representing the richness and divergence dimensions of the Pavoine–Bonsall scheme for classifying diversity metrics ([Pavoine and Bonsall, 2011](#); [Tucker et al., 2017](#)). Specifically, [Tucker et al. \(2017\)](#) proposed Faith's Phylogenetic Diversity (PD; [Faith, 1992](#)) and mean phylogenetic pairwise dissimilarity (MPD) as anchor metrics for the phylogenetic facet of diversity, while Functional Richness (FRic; [Villéger et al., 2008](#)) and functional MPD are two of the most commonly used metrics for representing functional diversity and divergence in ecology, respectively ([de Bello et al., 2016](#)). PD was calculated as the total length of all branches of taxa included in a community ([Faith, 1992](#)) using the R package "picante" ([Kembel et al., 2010](#)). FRic quantifies the extent of functional space filled by each community by calculating a convex hull containing all functional trait values of taxa found in the community ([Villéger et al., 2008](#)). It was calculated with the "dbFD" function of the "FD" package in R ([Laliberté et al., 2015](#); [Laliberté and Legendre, 2010](#)). We kept the first six axes of the principal coordinate analysis to reduce the multidimensionality of the functional space ([Leps et al., 2006](#)), following the suggestion of [Maire et al. \(2015\)](#). The latter authors have demonstrated that four axes are adequate for the representation of the functional space. Since the number of taxa occurring in the plots studied constitutes a constraint on the number of produced axes, only plots with six or more taxa were used. To make the metrics comparable, the PD and FRic indices were calculated using the presence/absence data because FRic cannot be calculated for abundance-weighted data ([Mouchet et al., 2010](#)). The ALL dataset included 3470 plots, and the UNDER dataset included 3449 plots. We tested the differences in the values of the functional and phylogenetic diversity metrics among the studied community types using Tukey's test.

To incorporate information on community composition and relative abundances of taxa using a metric appropriate for comparing functional and phylogenetic structure, we used the "melodic" function in R ([de Bello et al., 2016](#)) and calculated the mean pairwise, abundance-weighted dissimilarities for functional (MPDf) and phylogenetic (MPDp) diversity. Mean pairwise dissimilarity is the mean of dissimilarities in functional and phylogenetic distances between all pairs of taxa occurring within a plot. Square-root transformed abundance information was applied to avoid excessive weight of abundant taxa in the calculation of the functional structure index ([Májeková et al., 2016](#)). A functional distance was calculated using Gower's distance, while a phylogenetic distance was calculated as pairwise cophenetic distance in the phylogeny.

The standardised effect sizes of all the aforementioned metrics (hereafter called ses.FRic, ses.PD, ses.MPDf and ses.MPDp) were calculated as the deviation of the observed metric values from the expected values, derived from 999 random communities generated by the "richness" null model in the "picante" R package ([Kembel et al., 2010](#)). Null communities for the ALL dataset were built based on all vascular plant taxa, while null communities for the UNDER dataset were built only based on the non-phanerophyte taxa. All of these analyses were also performed for presence/absence data. The results were very similar to those derived from the abundance-weighted data, and are therefore not presented here. Moreover, the phylogenetic signal from the functional traits was tested for phylogenetic niche conservatism. Specifically, we tested the phylogenetic signal for each trait to check for phylogenetic niche conservatism. The phylogenetic signal was tested for all numerical and ordinal traits, as well as for the categorical traits with categories that could be converted to an ordinal scale. The phylogenetic signal test was conducted for the following traits: beginning of flowering, canopy height class, duration of flowering, leaf length, leaf ratio, life span, seed length, seed ratio, seed weight and seed storage behaviour. To test the phylogenetic signal, we calculated Pagel's  $\lambda$  ([Pagel, 1999](#)), which provides reliable results when the analysis is applied to phylogenetic trees that contain polytomies and suboptimal branch-length information, as

in the case of our phylogeny ([Molina-Venegas and Rodríguez, 2017](#); [Münkemüller et al., 2012](#)). This index assumes a classical Brownian motion (BM) evolutionary model. Its values vary from 0 to 1, with 0 indicating the absence of phylogenetic signal, while values close to 1 indicate trait evolution, according to BM. Pagel's  $\lambda$  was quantified using the "phylosig" function in the "Phytools" package in R ([Revell, 2012](#)).

### 2.3. Identifying congruences and incongruences between functional and phylogenetic diversity/structure patterns

Boosted regression trees (BRTs) was the main method used for testing the level of congruence between functional and phylogenetic diversity and structure. BRTs are statistical models that combine decision tree algorithms and boosting to increase model accuracy and performance ([Hastie et al., 2009](#)). They have better predictive power than most traditional modelling techniques ([Elith et al., 2008](#)) and tend to be robust to missing data and irrelevant input variables, while also being relatively easy to interpret and visualise ([Elith et al., 2008](#); [Hastie et al., 2009](#)).

BRTs were employed to model six different relationships between functional diversity and structure (the response variables) versus phylogenetic diversity and structure (the predictor variables). We also used community type as an additional predictor. We produced six BRT models: (1) functional diversity (FRic) as a function of the phylogenetic diversity (PD) and community type (ComType); (2) standardised functional diversity (ses.FRic) as a function of standardised phylogenetic diversity (ses.PD) and ComType; (3) and (4) equivalent to (1) and (2) but for the UNDER dataset, (5) standardised functional structure (ses.MPDf) as a function of the standardised phylogenetic structure (ses.MPDp) and ComType and (6) same as (5) calculated for the UNDER dataset. A similar set of six BRT models was also built with forest type being the second response variable instead of community type.

Median absolute errors (MAE) were used as a measure of model's overall predictive ability. Furthermore, the contribution (importance) of each predictor to model's prediction was implemented with a "feature importance" Monte Carlo permutation analysis ([Breiman, 2001](#)). Finally, partial dependence plots were used to show the average marginal effects of the two predictors on the outcome of each model ([Friedman, 2001](#)). The detailed methodology for building the BRT models and the resulting partial dependence plots are presented in [Appendix B](#).

In addition, contingency tables were created to represent the observed combinations of functional and phylogenetic structures across community types and forest types. Specifically, the ses.MPDf and ses.MPDp metrics were used in each plot to infer the assembly mechanisms that may have driven the observed functional and phylogenetic structure of community or forest types. Each sampling plot was assigned into one of three classes based on its functional or phylogenetic structure: clustered (ses.MPDf or ses.MPDp < -1.96); random (-1.96 ≤ ses.MPDf or ses.MPDp ≤ 1.96); or overdispersed (ses.MPDf or ses.MPDp > 1.96). This twofold, functional–phylogenetic classification leads to nine possible combinations for a plot. Based on these classes, 3 × 3 contingency tables were created by recording the percentage of sampling plots per community type or forest type belonging to each of the nine combinations for both ALL and UNDER datasets.

To check whether some of the structure classes were present in a particular forest or community type, we quantified the departure of the observed values from a random expectation for each contingency table using Monte Carlo permutation tests. If  $N$  is the number of instances in a specific forest type,  $N$  observed pairs of values of the two indices were randomly sampled with replacement from the pool of all forest types. This resampling removed any systematic association with forest type, but preserved the observed association between the two indices. The same resampling was additionally applied to community types instead of forest types. A new contingency table was created based on each resampling repetition, and the difference of observed minus resampled

class percentages between the tables was recorded. The final output of the resampling approach was a table of the mean departure of observed percentages from the random expectation from  $n = 1000$  resampling repetitions ( $\pm$  the confidence interval at a significance level  $\alpha = 0.05$ ).

### 3. Results

#### 3.1. Overall patterns of functional and phylogenetic indices

Analyses revealed a positive correlation between phylogenetic and functional diversity (PD – FRic) for both the ALL (Fig. 1A) and UNDER dataset (Fig. 1D), but no significant correlation between the standardised versions of the diversity and structure metrics (Fig. 1B and C and Fig. 1E and F, respectively). For both datasets, only random and overdispersed patterns were observed for phylogenetic structure, whereas only random and clustered patterns were observed for functional structure, except for two oak community types that had very few functionally overdispersed plots (Fig. 2). These general patterns differed between the two investigated datasets, with the UNDER dataset having more plots with non-random functional or phylogenetic structure (Fig. 2C and D).

Regarding the differentiation of functional and phylogenetic diversity and structure metrics among community types, according to Tukey’s test, community types differed more in terms of phylogenetic than functional diversity (PD and FRic) based on both the ALL and UNDER datasets (Appendix C). This pattern was also consistent for their standardised versions (ses.PD and ses.FRic) for the ALL dataset. Based on the UNDER dataset, community types differed more in terms of functional diversity (Appendix C).

Furthermore, all the investigated functional traits showed a statistically significant phylogenetic signal (Table 1). Half of the traits appeared to be highly conserved, with Pagel’s  $\lambda$  values close to 1, i.e. canopy height class and all the functional traits related to seeds (seed length, ratio, weight and storage behaviour). The rest of the traits had intermediate values of phylogenetic signal.

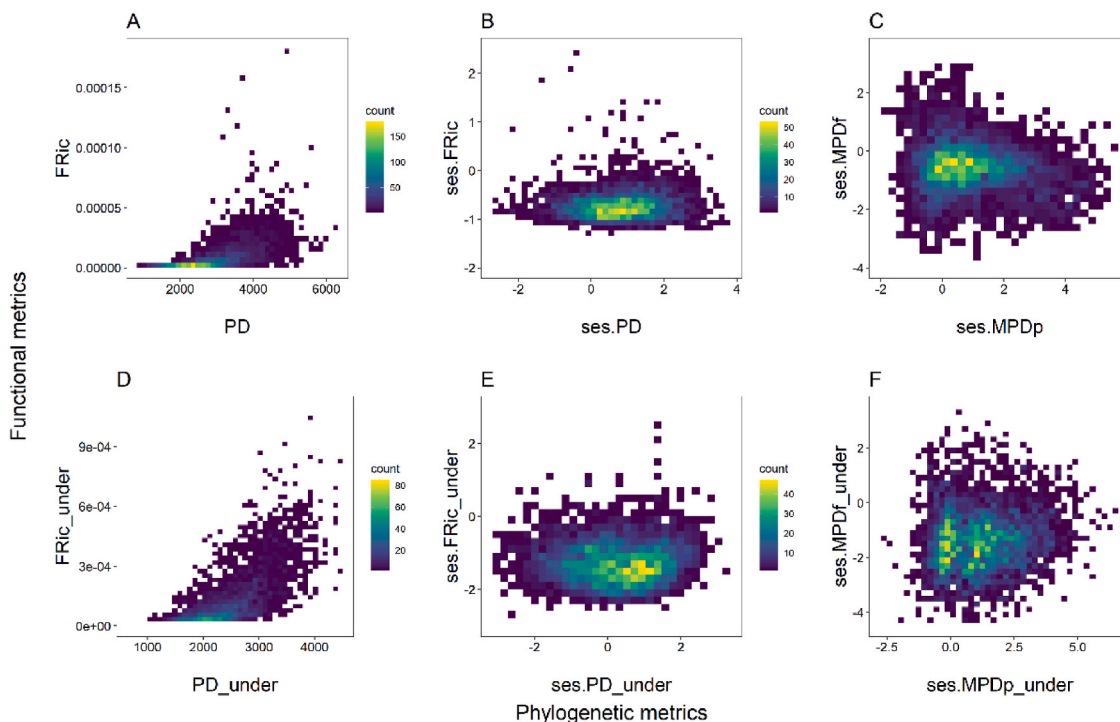


Fig. 1. Relation between the functional and phylogenetic diversity and structure metrics for the ALL (both canopy and understorey species; panels A, B and C) and UNDER (only understorey species; panels D, E and F) datasets.

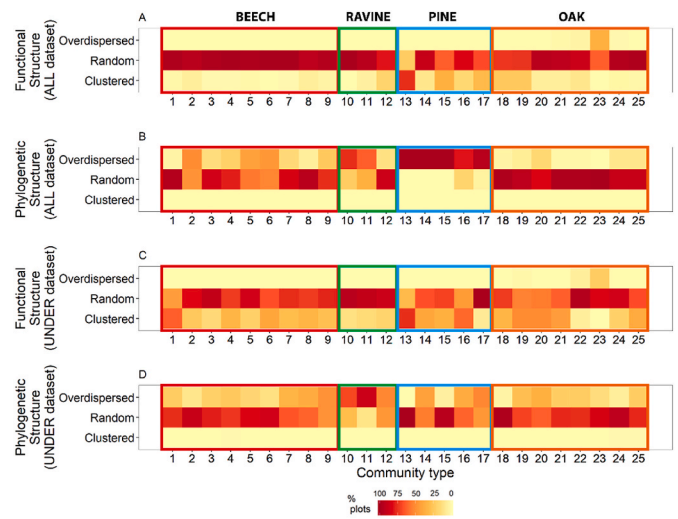


Fig. 2. Percentage of plots with clustered, random and overdispersed structure for each community type based on the ses.MPDf and ses.MPDp metrics for functional and phylogenetic structure, respectively. Panels A and B: Functional and phylogenetic structure from the ALL dataset; panels C and D: Functional and phylogenetic structure from the UNDER dataset. The coloured rectangles show the classification of community types in the four different forest types.

#### 3.2. Relationships between functional and phylogenetic facets

The performance of the BRT models was assessed by comparing the median absolute error (MAE) of each model’s predictions with the range of the response variable values on the test dataset (Table 2). Models (1)–(3) performed relatively well since the median absolute error of the predictions was relatively small compared with the values of the response variables in the test dataset (Table 2). Thus, phylogenetic diversity (PD and ses.PD) and community type were good predictors of functional diversity (FRic and ses.FRic) for the ALL dataset [Table 2;



**Table 1**

Pagel's  $\lambda$  values for the phylogenetic signal test of each functional trait studied. The level of statistical significance of the phylogenetic signal for all traits was  $p < 0.001$ .

Functional trait	Pagel's $\lambda$
Beginning of flowering	0.69
Canopy height class	0.93
Duration of flowering	0.32
Leaf length	0.64
Leaf ratio	0.34
Life span	0.46
Seed length	0.98
Seed ratio	0.84
Seed weight	0.99
Storage behaviour	0.99

**Table 2**

Formulas of individual boosted regression tree models, range of the response variable values in the test dataset, and median absolute error (MAE) of each model's predictions. Response variables are functional richness (FRic), its standardised equivalent (ses.FRic), and standardised functional structure (ses.MPDf). Predictor variables include phylogenetic diversity (PD), its standardised equivalent (ses.PD), standardised phylogenetic structure (ses.MPDp), and community type (CommType).

ID	Model formula	Response test values (min–max)	MAE of predictions
(1)	FRic ~ PD + CommType	$2.39 \cdot 10^{-9}$ – $1.59 \cdot 10^{-4}$	$1.86 \cdot 10^{-6}$
(2)	ses.FRic ~ ses.PD + CommType	–1.21–2.04	0.12
(3)	FRic_under ~ PD_under + CommType	$2.96 \cdot 10^{-8}$ – $9.15 \cdot 10^{-4}$	$2.45 \cdot 10^{-5}$
(4)	ses.FRic_under ~ ses.PD_under + CommType	–2.61–0.66	0.3
(5)	ses.MPDf_all ~ ses.MPDp_all + CommType	–3.22–2.57	0.513
(6)	ses.MPDf_und ~ ses.MPDp_und + CommType	–4.36–3.24	0.54

models (1) and (2)]. For the UNDER dataset, this was true for the non-standardised version of PD (PD\_under) but not for its standardised version (ses.PD\_under) [Table 2; models (3) and (4), respectively]. In addition, the relatively high median absolute errors of models (5) and (6) indicate that community type and, in particular, phylogenetic structure (ses.MPDp) are not reliable predictors of functional structure (ses.MPDf) for any of the datasets (Table 2). The average marginal effects of each pair of predictors on the predicted outcome for each model are shown in the partial dependence plots in Appendix B.

Higher predictor importance was found for phylogenetic diversity than for community type for models (1) and (3), indicating that functional diversity (not standardised for species richness) was better predicted by phylogenetic diversity than by community type (Fig. 3). In the remaining models, community type had a higher predictor importance indicating that ses.FRic, ses.FRic\_under, ses.MPDf and ses.MPDf\_under are better predicted by community type than ses.PD, ses.PD\_under, ses.MPDp and ses.MPDp\_under, respectively. Thus, although functional and phylogenetic diversity of forest plots are significantly correlated, this seems to be mainly due to species richness (Fig. 3).

Interesting patterns emerged from investigating the combinations of functional and phylogenetic structures across community types and forest types through contingency tables. Only the contingency table of results for the forest type level and from the UNDER dataset is presented here (Table 3). The results for the community type level from the UNDER dataset were generally consistent with the results for the forest type level (Appendix D, Table D2). The corresponding results based on the ALL dataset revealed fewer functionally and phylogenetically structured plots (Appendix D, Tables D1 and D3). Of the nine possible structure classes, four were observed more commonly in our dataset,

namely random phylogenetic structure combined with clustered functional structure, random phylogenetic structure combined with random functional structure and overdispersed phylogenetic structure combined with random functional structure. The other six structure classes were observed in very few cases or not at all.

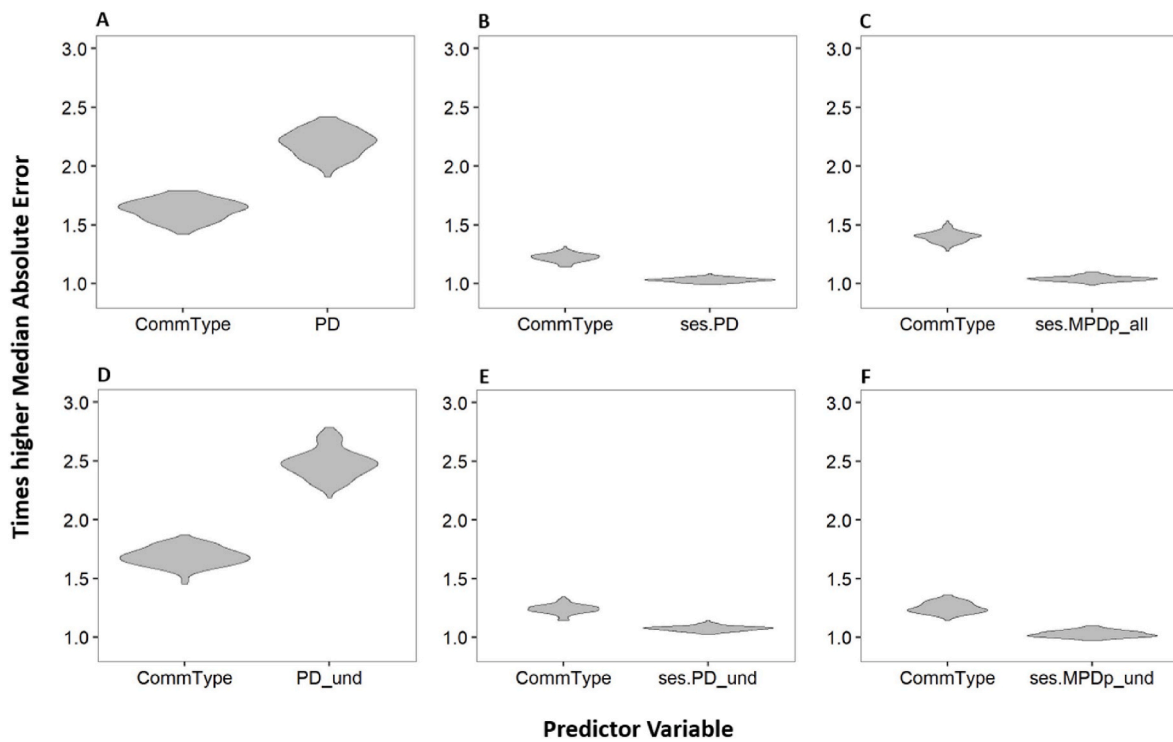
The occurrence frequency of each structure class varied among the forest types studied. A stronger deviation of community structure from random expectations was found for ravine and, to a lesser extent, for pine forests compared to beech and oak forests (Table 3). Ravine forest plots were phylogenetically overdispersed and functionally random significantly more frequently than under random expectation; at the same time, phylogenetically random and functionally clustered plots were observed significantly less often than expected. Pine forest plots were phylogenetically random and functionally clustered significantly more often than expected, while fewer plots of this forest type were randomly structured for both diversity facets.

#### 4. Discussion

Our study revealed complex patterns of functional and phylogenetic diversity and structure among 25 deciduous broadleaved and mountainous coniferous forest community types in northern and central Greece. Differences in community structure were observed among the forest types, namely beech, ravine, oak and pine forests. We found a significant relationship between functional diversity, phylogenetic diversity and community type, with phylogenetic diversity predicting functional diversity better than community type. In contrast, the relationship of functional structure with phylogenetic structure and community type was not strong. Separate investigation of two datasets, one including all taxa found in the forest vegetation plots and the other including only taxa from the understorey, revealed differences between observed patterns of structure when tree taxa were included in the analysis. Therefore, it provided additional information on the assembly mechanisms of the Greek forest community types.

##### 4.1. Congruence (or lack of it) between functional and phylogenetic diversity and structure

Previous ecological studies have simultaneously incorporated phylogenetic and functional diversity metrics, using different methods depending on the specific research questions as well as data availability and properties. Cadotte et al. (2019) summarised four approaches that have been primarily used by researchers to incorporate the simultaneous study of phylogenetic and functional diversity patterns, including the investigation of the phylogenetic signal of the functional traits used, investigation of the correlation between the two diversity facets, comparison of functional and phylogenetic structure of communities and an indirect approach of exploring the response of the two diversity facets to other variables (e.g. environmental gradients). In the present study, we employed the first three direct approaches of simultaneously incorporating functional and phylogenetic facets. Although we found phylogenetic conservatism of the traits used and a positive correlation between phylogenetic and functional diversity, we observed a lack of congruence between functional and phylogenetic dispersion patterns. More specifically, we found high or at least moderate phylogenetic conservatism for all traits studied and a positive relationship between functional and phylogenetic diversity, both for the understorey and for the whole community. These patterns are consistent with most of similar studies that have investigated these two diversity facets simultaneously (Cadotte et al., 2019). However, incongruent patterns of functional and phylogenetic patterns were observed. Overall, random structure, functional clustering and phylogenetic overdispersion were the predominant patterns in the vegetation plots investigated in this study. The two facets of diversity led to the observation of opposite assembly structures (clustered for functional and overdispersed for phylogenetic), but these patterns were rarely observed for the same plots. On the contrary, when



**Fig. 3.** Predictor importance plots for each boosted regression model. The response variables are: (A) FRic; (B) ses.FRic; (C) ses.MPDf\_all; (D) FRic\_under; (E) ses.FRic\_under; and (F) ses.MPDf\_under. Each violin plot shows the normalised distribution of predictor importance from  $n = 100$  shufflings of the predictor. For each predictor variable in each model, we show how many times higher the median absolute error (MAE) is when the predictor is shuffled compared with the original MAE of unshuffled predictors (Appendix B).

**Table 3**

Contingency tables showing the percentages of plots assigned to one of the nine possible structure classes for each forest type separately based on the UNDER dataset. The departure of the observed percentages of plots per structure class from the random expectation is shown in parentheses. For example, 5.52 (−1) means that 5.52% of N plots in beech forests were functionally clustered and phylogenetically overdispersed, and that this observed percentage was on average 1% lower than expected if forest type had no effect (average of  $n = 1000$  resamplings of N plots from the whole dataset, regardless of forest type).

		Functional structure					
		Clustered		Random		Overdispersed	
Phylogenetic structure		<b>BEECH</b>					
	Clustered	0.06	(+0)	0	(+0)	0	(+0)
	Random	23.88	(+0)	50	(+1)	0	(−1)
	Overdispersed	5.52	(−1)	20.54	(+0)	0	(+0)
		<b>RAVINE</b>					
	Clustered	0	(+0)	0	(+0)	0	(+0)
	Random	<b>8.16</b>	(−15)	<b>26.94</b>	(−22)	0	(−1)
	Overdispersed	7.76	(+1)	<b>57.14</b>	(+36)	0	(+0)
		<b>PINE</b>					
	Clustered	0	(+0)	0	(+0)	0	(+0)
	Random	<b>31.94</b>	(+9)	<b>39.27</b>	(−10)	0	(−1)
	Overdispersed	7.85	(+2)	20.94	(+0)	0	(+0)
	<b>OAK</b>						
Clustered	0	(+0)	0.16	(+0)	0	(+0)	
Random	24.65	(+1)	52.99	(+4)	1.56	(+1)	
Overdispersed	6.55	(+0)	<b>13.76</b>	(−7)	0.33	(+0)	

a plot was structured for one diversity facet, it was usually random for the other facet, as already observed in several studies (Cadotte et al., 2019). Cadotte et al. (2019) mention several issues that may account for such incongruences, including possible differential effects of scale on the two diversity facets, the identity and quantity of the functional traits included, and methodological issues related to the singular nature of the measure of phylogenetic diversity in comparison with the multivariate measures employed for functional diversity.

Here, we argue that phylogenetic diversity should not be employed as a proxy of functional diversity for inferring community assembly mechanisms because phylogenetic relatedness is not always a good

predictor of ecological similarity (Losos, 2008). On the contrary, the incongruences between functional and phylogenetic patterns highlight the importance of studying these biodiversity facets simultaneously (Cadotte et al., 2019). Significant phylogenetic signal of the investigated traits, which is considered to allow confident inferences about community assembly (Cavender-Bares et al., 2009; Webb et al., 2002), combined a weak correlation between phylogenetic and functional diversity patterns, were also found by Doxa et al. (2020) and attributed to phylogenetic relatedness of functionally similar species for only certain clades of the phylogenetic tree.

For all the standardised metrics, we found that community type had

better predictive power for functional structure than the corresponding metrics of phylogenetic structure, in agreement with recent studies that have revealed distinct functional and phylogenetic patterns between different assemblages or habitat types due to habitat differentiation (González-Caro et al., 2014; Micó et al., 2020). Therefore, for a better investigation of biotic interactions and local environmental filters driving community assembly, a community-level analysis might be more appropriate than a grid-level analysis (Bruehlheide et al., 2018), which is also supported by the present study. The contrasting patterns of community structure may also be related to the late-successional stage of these community types. The mountain forests investigated here were functionally either random or clustered and phylogenetically either random or overdispersed, which is in agreement with previously observed patterns of other late-successional forests (Chun and Lee, 2019; Ding et al., 2012; Letcher, 2010).

#### 4.2. Differences between forest layers and forest types

Patterns of phylogenetic and functional diversity and structure were found to differ between the vegetation layers studied and among forest types, in agreement with the findings of previous studies (Augusto et al., 2015; Chai et al., 2016). Specifically, the investigation of the phylogenetic and especially functional diversity and structure of the forest understorey revealed patterns that were not detected in analyses of all taxa, including trees and shrubs. More communities were found to be functionally structured (mainly clustered) in the understorey dataset, possibly due to the differing microhabitat conditions among community types that depend on their canopy composition (Barbier et al., 2008). In addition, more communities were found to be phylogenetically structured (mainly overdispersed) in the understorey dataset. In this case, the exclusion of woody taxa (characterized by a distinct evolutionary histories) allowed the evolutionary differences of herb-layer taxa to become more apparent.

The predominant structure class (combination of functional and phylogenetic structure observed for each plot) differed among understoreys of the four forest types. Functional and phylogenetic randomness was observed most frequently in three of our four forest types, suggesting that mechanisms such as dispersal or neutral assembly constitute the main assembly rule (Kraft et al., 2007; Pavoine and Bonsall, 2011). However, the observation of random structure due to the simultaneous presence of multiple biotic and abiotic factors, leading to a balance between environmental filtering and limiting similarity, cannot be ruled out for such complex systems (Pavoine and Bonsall, 2011; Spasojevic and Suding, 2012). The next most common class (observed in over 40% of beech, pine and oak plots) was the combination of functional clustering with phylogenetic randomness, suggesting a strong prevalence of biotic or abiotic habitat filtering. Habitat filtering rather than environmental filtering has been suggested because the latter is known to have stronger effects on the overstorey layer of forest communities (Chai et al., 2016; Lagerström et al., 2013), but we observed filtering effects only when overstorey taxa were excluded from the analysis. Habitat filtering, as a result of understorey microhabitat differentiation among forest types, is supported because herbaceous taxa are known to have edaphic and microhabitat-dominated niches in the understorey (Chai et al., 2016). For example, Augusto et al. (2015) documented several significant differences in the effects of evergreen gymnosperms on forest functions compared to those of deciduous angiosperms, which may be responsible for creating different microhabitats of pine forest types, leading to functional clustering when analysed with broadleaved forests, in agreement with our findings. Furthermore, ravine forests differed significantly from the patterns of beech, oak and pine forests. They had the fewest randomly structured plots, a relatively high number of functionally random and phylogenetically overdispersed plots, and a very small number of functionally clustered and phylogenetically random plots. The lack of functional clustering indicates that more functionally dissimilar species coexist in this forest type than in the

other forest types. The prevalence of such a distinct functional and phylogenetic structure compared to surrounding forest types suggests long-term environmental stability and a refugial character of ravine forests (Keppel et al., 2018).

## 5. Conclusions

Consistent with cases previously observed in the literature (Cadotte et al., 2019), the functional traits used in our study were found to be phylogenetically highly to moderately conserved, and phylogenetic and functional diversity were positively correlated. Nevertheless, phylogenetic structure was not a good predictor of functional structure. The most common patterns found across the datasets used were random structure for both diversity facets, random phylogenetic structure combined with clustered functional structure and overdispersed phylogenetic structure combined with random functional structure. Thus, our findings are consistent with the review by Cadotte et al. (2019), which demonstrated that contradictory signals of community structuring mechanisms based on these two diversity facets are common (observed in nearly half of the reviewed studies). Interpretation of such mechanisms becomes even more complicated in the case of forest communities, since our results indicated partially different assembly mechanisms between forest layers. In particular, we found that the whole forest communities (including all forest layers) mostly exhibited random structure, whereas the understorey vegetation layer was more often subject to deterministic processes. Finally, habitat types were shown to be an important variable in community assembly research since, in the present study, their consideration allowed to identify patterns of phylogenetic and functional structure patterns.

### Authors' contributions

Conceptualization, AM and IT; Data Curation, AM; Methodology, AM, DK, MC, AK, IT; Formal Analysis, AM and DK. Writing – Original Draft Preparation, AM; Writing – Review & Editing, AM, DK, MC, AK, IT.

### 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

### Data availability

Data will be made available on request.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.actao.2023.103933>.

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