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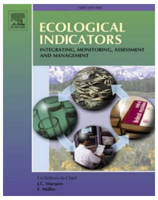

Original Articles

Plant trait filtering is stronger in the herb layer than in the tree layer in Greek mountain forests

Anna Mastrogianni[a,*], Milan Chytrý[b], Athanasios S. Kallimanis[c], Ioannis Tsiripidis[a]

[a] Department of Botany, School of Biology, Aristotle University of Thessaloniki, Thessaloniki GR-54124 Greece
[b] Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic
[c] Department of Ecology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki GR-54124, Greece

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ABSTRACT

We studied the differentiation among plant communities of deciduous broadleaved and mountain coniferous forests in terms of functional diversity and identity at a regional scale (northern and central Greece). We asked if patterns of functional differentiation among communities are consistent between the overstorey and understorey layers and if they can be influenced by deep past environmental conditions. Functional Richness (FRic) and Functional Dispersion (FDis), as well as their standardized effect sizes, were employed to assess the multivariate functional diversity of the community types. In contrast, single-trait Community Weighted Means (CWMs) were used as surrogates of functional identity. The aforementioned indices were calculated for three datasets, namely all the vascular plant taxa found in individual vegetation plots (total community), all phanerophyte (tree and shrub) taxa (overstorey) and all non-phanerophyte vascular plant taxa (understorey). We found that community types and especially four broad forest types (beech, ravine, pine and oak forests) are well differentiated in terms of functional composition (identity), as indicated by Non-Metric Multidimensional Scaling (NMDS). After conducting an NMDS for the three datasets, functional identity based on the total floristic composition was found to be the best discriminator of the studied communities. However, contrasting patterns were found for some specific traits or their categories between overstorey and understorey layers. The patterns of functional diversity of the community types (based on multivariate indices), revealed by calculating the standardized effect sizes of FRic and FDis based on the richness null model, did not differ substantially from random expectations for most of the studied community types when the dataset of all the vascular plant taxa was analyzed. However, the patterns revealed for the overstorey layer differed from those for the understorey layer. For the latter layer, the clustered structure was revealed in many community types based on the ses.FDis metric. Indications of deep past influence on the functional composition were found for certain community types (i.e. ravine forests) based on single-trait metrics, but no indication of such influence was found based on multivariate indices. Our findings highlight the complementarity and the additive explanatory value of the simultaneous use of single- and multi-trait approaches and their application to different layers in forests.

1. Introduction

A fundamental goal in ecology is to understand the processes and mechanisms influencing spatial patterns of species diversity in natural communities. Towards this direction, functional trait information derived from morphological, physiological, and phenological characteristics of species is employed to study the relationships between these characteristics and environmental variation, community structure and ecosystem processes (Brockerhoff et al., 2017; Laughlin et al., 2012; Menge and Chazdon, 2016).

It is widely accepted in functional ecology that strong environmental stress usually leads to decreased functional diversity, while the prevalence of competitive exclusion leads to its increase (Weiher and Keddy, 1995). In addition, functional overdispersion (i.e. communities with co-occurring species that are functionally less similar to each other than expected in random communities) is considered to result from niche partitioning or limiting functional similarity (Kluge and Kessler, 2011). In contrast, under environmental filtering, a pattern of functional

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* Corresponding author.
E-mail addresses: amastroi@bio.auth.gr (A. Mastrogianni), chytry@sci.muni.cz (M. Chytrý), kalliman@bio.auth.gr (A.S. Kallimanis), tsiripid@bio.auth.gr (I. Tsiripidis).

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clustering (or underdispersion, i.e., communities with co-occurring species that are functionally more similar to each than expected in random communities) is assumed to result from the selection of species with particular habitat affinities or resource requirements (Cavender-Bares et al., 2009). Nevertheless, contrasting patterns of abiotic stress leading to high levels of functional diversity have also been documented, and other processes (e.g. facilitation) have been suggested to affect patterns of functional diversity (Spasojevic and Suding, 2012).

In addition to functional diversity, functional trait composition (i.e. functional identity) has been acknowledged during the last years to contribute towards a better understanding of ecosystem processes, community assembly rules and other related ecological questions (Dias et al., 2013). Functional diversity reflects the niches filled by the community members (Petchey and Gaston, 2006; Villéger et al., 2008), while functional identity is considered to reflect the locally optimal trait strategy given the environmental conditions of a site (Shipley, 2009). There is increasing evidence that the simultaneous use of functional diversity and identity metrics can help answer the questions concerning the relations between biodiversity and ecosystem functioning (Dias et al., 2013; Li et al., 2017; Weigel et al., 2016). On the one hand, functional diversity metrics simultaneously incorporate multiple traits in order to capture potential syndromes within the functional space of an ecological community (Mouchet et al., 2010) that can occur due to interspecific interactions (e.g. competition, mutualism, facilitation) or imprints from (past or present) environmental factors and processes (see Dias et al., 2013; Mouchet et al., 2010). On the other hand, CWM is a single trait measure that captures the most prevailing trait value or category in an ecological community, reflecting the strong effects of dominant species on ecosystem processes (Grime, 1998).

In the studies of ecosystem processes, decisions regarding not only the type of employed metrics (diversity or identity) but also the different groups of species (e.g. taxonomic groups or growth forms) to be involved in the analysis can significantly affect the unravelled patterns of functional diversity. In forest ecosystems, such unique patterns are expected to occur due to discrete forest layers constituted by taxa of distinct life forms. In particular, canopy structure and density of the dominant species have been suggested to affect understorey species by resource filtering effects or by protection from wind, cold or drought (Milcu et al., 2016; Prescott, 2002; Spasojevic and Suding, 2012). There is recent evidence that diversity patterns of forest ecosystems can be particularly complex due to the presence of distinct overstorey and understorey layers which may be subjected to different assembly mechanisms (Luo et al., 2019b; Zhang et al., 2017).

Many studies investigating functional diversity patterns at broad spatial scales have been based on grid data of species occurrence (Swenson et al., 2012; Thuiller et al., 2006; Tsianou and Kallimanis, 2020). Bruelheide et al. (2018) were the first to prepare a worldwide vegetation-plot dataset and use it to test the dominant structuring processes of community trait composition at the global scale. Vegetation-plot data distributed over broad spatial scales can capture crucial information regarding species distribution across scales and community assembly patterns at fine scales. Furthermore, Damschen (2018) stressed the need for empirical tests of potential dependencies between functional traits, biotic and abiotic drivers, and community assembly mechanisms. Depending on the spatial scale of the dataset, several levels and filters are involved in the interpretation of community assembly, integrating evolutionary and ecological concepts. Such concepts include neutral processes and environmental filtering across large spatial scales and niche structuring and demographic processes at finer scales (Chesson, 2000; Kraft et al., 2008; 2015; Weiher et al., 2011). Additionally, processes extrinsic and intrinsic to a community affect community assembly differently, with the first mainly affecting the global species pool and the type and abundance of the arriving biological units in a community, and the latter determining the final community composition and relative abundances (Pearson et al., 2018).

In this study, the ecosystems of broadleaved deciduous and mountain coniferous forests of the mountainous part of northern and central Greece are investigated. This topographically and climatically variable area has been considered a glacial refugium for different forest species and forest community types (Gavin et al., 2014; Mastrogianni et al., 2019; Papageorgiou et al., 2014; Tzedakis et al., 2013). Location of glacial refugia must have significantly shaped the current diversity patterns. The regional filtering of species pools and non-random extinctions constitute the main mechanisms through which historical climatic conditions may have lasting imprints on current patterns of functional diversity (Mouillot et al., 2013; Ordonez and Svenning, 2016; Zanne et al., 2014). Such evidence of impacts of past environmental conditions on the present-day species trait spectra, subsequently affecting the composition of current plant communities, constitutes an important finding of the work of Bruelheide et al. (2018) (see also Damschen, 2018).

The present study employs indicators of functional diversity and identity to determine if forest community types in the study area are characterized by different functional patterns. We investigated functional diversity and identity differentiation in the main vegetation layers (overstorey and understorey) as well as in the total floristic composition to test if different patterns exist. In doing so, we hypothesise that:

1. Patterns of functional diversity and identity differ between forest community types.
2. Patterns of functional diversity and structure differ between overstorey and understorey layers of community types.
3. At least some community types in our putative refugial area have special patterns of functional diversity (absence of functional clustering or even functional overdispersion) or distinct characteristics of functional identity, which may constitute an imprint of past environmental conditions on the current functional attributes of plant communities.

2. Methods

2.1. Study area

Patterns of functional diversity and identity of deciduous broadleaved and mountain coniferous forest community types of northern and central Greece were investigated. From the 13 floristic regions of Greece, defined based on floristic differences, biogeographical barriers and environmental (mainly climatic) patterns (Strid and Tan, 1997), five regions, namely North East (NE), North Central (NC), East Central (EC), North Pindos (NPi) and South Pindos (SPi), were selected as our study area. The main mountain ranges from which vegetation plots were investigated are shown in Appendix A; Figure A.1.

2.2. Vegetation data and classification

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) were revised and extended through new sampling and addition of all the bibliographic data available for deciduous broad-leaved and mountain coniferous forests in the study area. Subsequently, 3493 vegetation plots were selected as representative of these forests in the study area. This dataset is highly representative of the overall diversity of the investigated forest types in the study area, as demonstrated in Appendix A. The vegetation plots were sampled from 1967 to 2017 and had a mean altitude of 994 m (SD = 379 m). Despite the long period during which the plots were sampled, inferences regarding any potential effect of climate change on community composition are not discussed in the present study since our questions refer to patterns of observed diversity and its differentiation over time. Species taxonomy and nomenclature were unified according to the Euro + Med PlantBase (Euro+Med 2006-2021), while 20% of taxa derived from merging infraspecific taxa to the species level. The final list of taxa included 43, 10 and 877 taxa at the genus, aggregate and species levels, respectively, and 12 taxa representing a combination of two species that were difficult to identify (e.g. *Viola reichenbachiana* et *V. riviniana*). Abundance information was available for all the plots as ordinal cover classes (most plots were recorded using the Braun-Blanquet scale and a few plots using the Londo scale). The ordinal classes were transformed to the average percentage covers of each class. For abundance-weighted calculations, this percentage was raised by a power of 0.2 to reduce the effect of dominant species. After excluding 610 (38.7%) taxa with fewer than five occurrences in the dataset, 965 taxa remained and were used for vegetation classification. Taxon occurrences across different layers were merged using the formula in the JUICE program that assumes random overlap of covers of species individuals in different layers (Fischer, 2015; Tichý, 2002). The plots were subsequently classified by TWINSPAN (Hill, 1979) and modified TWINSPAN (Roleček et al., 2009), resulting in 25 community types. The identified community types were floristically differentiated by unique combinations of diagnostic taxa, reflecting mainly the distribution of the community types along the environmental gradients of temperature, nutrient availability, moisture and soil reaction, as well as partly their geographical distribution. A more detailed description of dataset preparation and vegetation classification is provided in Mastrogianni et al. (2019).

2.3. Environmental conditions

We used Ellenberg indicator values (Ellenberg et al., 1991) to capture the differentiation of the environmental conditions among plots. The Ellenberg indicator values have the advantage of characterizing environmental conditions prevailing strictly within each vegetation plot at the time of sampling or shortly before. For each plot, we calculated the indicator value for light, temperature, moisture, reaction, and nutrient availability as the average of the indicator values of all the taxa present in each plot, weighted by their abundance (midpoints of percentage cover of the grades of the Braun-Blanquet scale, raised by a power of 0.2). For 22% of taxa, there was no Ellenberg indicator value available. For each taxon without indicator value, we identified four taxa with the highest percentage co-occurrence in the dataset (at least 65%) and calculated their mean value. In cases with less than four taxa with such a high percentage of co-occurrences, fewer taxa were used. To test for the relationships between Ellenberg indicator values and the functional diversity indices, the Pearson correlation coefficient was employed. However, both the values of functional diversity metrics and Ellenberg indicator values are derived from species composition and thus are not independent of each other. Therefore, the statistical significances of these correlations were not tested because P-values would be inflated (Zelený, 2018). Finally, to test for the relationships between Ellenberg indicator values and the functional traits and trait categories, the *test_cwm* function in the weimea package (Zelený, unpublished, https://github.com/zdealveindy/weimea) was used. Spearman's correlation coefficient and the statistical significance of correlations were calculated by applying the modified (column-based) permutation test (Zelený, 2018).

2.4. Functional trait selection

An initial extensive search for available trait information was conducted in a large number of databases and floristic literature (Appendix B), and information regarding 21 traits was collected, with a special effort given in order to collect traits related to different plant organs (e.g., stem, leaf, flower, seed). Despite the potential additive value of belowground traits, information was available for a very small percentage of taxa occurring in our dataset; therefore, they were excluded from the dataset. After testing for correlations between traits and conducting preliminary analyses, a database of 16 functional traits concerning vegetative (canopy height class, canopy structure, leaf length, leaf persistence, leaf length/width ratio, life form, life span) and generative characteristics of taxa (beginning of flowering, colour of flower, dispersal mode, duration of flowering, pollen vector, seed length, seed length/width ratio, seed weight, seed storage behaviour) was created based on information collected from the literature (Table 1; Appendix B). These traits were selected to provide insight into three

Table 1
Functional traits employed in the present study, their functional role and the level of completeness after the gap-filling. For each functional trait, the type of the variable [categorical (C), numerical (N) or ordinal (O)] is presented as well as the different classes of the trait. Abbreviations of the functional traits and their classes are in parentheses.

Functional trait	Type and classes of the variable	Function	Completeness
Beginning of flowering (BF)	C: autumn (aut), early spring (esp), spring (sp), summer (sum)	Reproduction	94.7%
Flower colour (FC)	C: blue/lilac/violet (blue), brown/green (green), orange/yellow (yellow), pink/purple/red (pink), white (white), no flower (no)	Reproduction	100%
Dispersal mode (DI)	C: autochoric (aut), hemerochoric (hem), meteorochoric (wi), nautochoric (wa), zoochoric (zoo), other (oth)	Dispersal	97.8%
Duration of flowering (DF)	O	Reproduction	94.7%
Pollen vector (PV)	C: cleistogamy (cl), geitonogamy (gei), insects (in), selfing (sel), water (wa), wind (wi)	Reproduction	90.9%
Seed length (SL)	N	Dispersal	94.7%
Seed length/width ratio (SR)	N	Dispersal	94.7%
Seed weight (SW)	N	Dispersal	99.0%
Storage behaviour (ST)	C: intermediate (int), orthodox (or), recalcitrant (rec)	Dispersal	93.2%
Canopy height class (CHC)	O; $\mathbf{1} < 0.1$, $0.1 \le \mathbf{2} < 0.3$, $0.3 \le \mathbf{3} < 0.6$, $0.6 \le \mathbf{4} < 1$, $1 \le \mathbf{5} < 3$, $3 \le \mathbf{6} < 4$, $4 \le \mathbf{7} < 15$, $15 \le \mathbf{8}$ (m)	Competitiveness, Stress tolerance	99.9%
Canopy structure (CS)	C: leaves distributed regularly along the stem (reg), rosette (ros), semi-rosette (sros), scarcely foliated (sc), tufts and crowns on the top of taller shoot/vegetative stem (tuf)	Competitiveness, Stress tolerance	100%
Leaf length (LL)	N	Competitiveness, Stress tolerance	99.2%
Leaf length/width ratio (LR)	N	Competitiveness, Stress tolerance	99.2%
Leaf persistence (LP)	C: overwintering (wi), persistent green (per), spring green (sp), summer green (sum), no leaves (no),	Competitiveness, Stress tolerance	97.0%
Life form (LF)	C: chamaephyte (C), geophyte (G), hemicryptophyte (H), phanerophyte (P), therophyte (T)	Competitiveness, Stress tolerance	100%
Life span (LS)	C: annual (an), biennial (bi), perennial (pe)	Competitiveness, Stress tolerance	100%

central processes involved in community assembly, namely reproduction, dispersal and competition (Table 1) (Kraft and Ackerly, 2014). Dispersal-related traits are essential for determining species mobility and location in the landscape and their ability for a successful establishment (Hargreaves and Eckert, 2014). For example, dispersal mode provides information on species adaptations to biotic and abiotic vectors (Eriksson and Kiviniemi, 2001), while seed traits are linked with the critical life stage of germination, which at least partly drives plant community assembly (Larson et al., 2015). On the one hand, seed shape partly determines the speed of germination (Bu et al., 2016) and is predictive of persistence in soil seed banks (Thompson et al., 1993). On the other hand, seed mass is related to seed dispersal, establishment, competition, frost tolerance and plant growth rates (Turnbull et al., 1999; Weiher et al., 1999; Westoby et al., 2002). Finally, reproduction-related traits have a key role in species fitness (E-Vojtkó et al., 2020), while the timing of reproductive events determines the trade-off between vegetative and reproductive growth (Bolmgren and Cowan, 2008; Elzinga et al., 2007), and flower colour and pollination mode can largely affect pollen transfer efficiency and thus overall reproductive success (Scopece et al., 2015).

Gap-filling was applied with missing values of numerical data being replaced by the mean of the available trait values for the taxa belonging to the same genus, while for categorical data gap-filling was only applied when all the taxa in the same genus with available trait information had the same value (Shan et al., 2012). The level of data completeness after the gap-filling procedure is shown in Table 1. We excluded from the dataset taxa with four or fewer occurrences and taxa taxonomically identified at the genus and family level. The final trait matrix included 16 functional traits and 923 taxa.

2.5. *Functional diversity and identity in different vegetation layers*

To investigate if the patterns of functional diversity and identity differ between overstorey and understorey layers of community types, all the analyses were performed for three different datasets. The first dataset included all the vascular plant taxa present in a plot (ALL dataset). The other two datasets were subsets of the ALL dataset. The second dataset represented the overstorey layer of the plots (OverSt dataset) and was constituted only of the phanerophyte (tree and shrub) taxa plots. Since some metrics require at least three species occurrences to be calculated, 554 plots (16%) of the original dataset that included less than three phanerophyte taxa were omitted from this analysis. Finally, the third dataset represented the understorey layer of the plots (UnderSt dataset) and included all the taxa with life form other than phanerophyte (i.e. chamaephytes, geophytes, hemicryptophytes, therophytes).

2.6. *Functional identity*

The functional identity was quantified by means of the Community Weighted Means (CWM) metric. CWM values per plot were computed for each trait as the mean trait value of all species weighted by their relative importance for both numerical and categorical traits, using the *functcomp* function of the FD package in R software (Lavorel et al. 2008; Laliberté and Legendre 2010; Laliberté et al. 2015). For this analysis, the data tables of plots × species and species × functional trait values were employed. Taxon abundances were used for the calculation of the CWMs after their square-root transformation. For the case of numerical traits, CWM values express abundance-weighted mean value for the species present in a plot or a community. In contrast, for categorical traits, CWM values express the percentage of relative abundance of each factor level of the categorical trait. The average of CWMs of all the plots classified in each forest community type was used as the CWM value at the level of the community type. Furthermore, standardized effect sizes of CWMs for all traits were calculated by creating 999 random community data matrices from the regional species pool of the 923 taxa with the richness null model by employing the *randomizeMatrix* function of the picante package in R (Kembel et al., 2010). A community type was considered to have a statistically significant pattern when more than 30% of their plots differed from random expectations.

Based on these community-type level CWM values of the 25 community types (matrix of 16 traits and their categories × 25 community types) a non-metric multidimensional scaling (NMDS; function *metaMDS* in package vegan; Minchin, 1987; Oksanen et al., 2016) was performed to identify differences between the functional identity of the investigated community types. More specifically, for this analysis, the data table of community types × CWM value per functional trait was employed. The NMDS was performed using the Bray-Curtis distance with 100 random starts. Pearson correlation coefficient was used to test for relationships between the NMDS axes and the CWMs of traits.

2.7. *Functional diversity*

Two multivariate indices of functional diversity were employed for the investigation of multidimensional functional diversity patterns of forest community types in Greece, namely functional richness (FRic) (Villéger et al. 2008) and functional dispersion (FDis) (Laliberté and Legendre 2010). The combined study of these metrics allows the estimation of the functional space occupied by the taxa present in a community and the distance of the taxa from the centroid of this functional space (Mason et al., 2005).

Similarly to CWM, for the calculation of FRic and FDis the data tables of plots × species and species × functional trait values were employed. Gower's distance was used to calculate a trait-based distance matrix due to its ability to handle missing values. Principal Coordinate Analysis was used to reduce the multidimensional functional space to a set of uncorrelated traits (Lepš et al., 2006). To maintain an adequate number of dimensions of functional space (Maire et al., 2015), we aimed at keeping the first six axes of the PCoA for the estimation of functional diversity indices. Because the number of employed axes is constrained by the species richness of the taxonomically poorest sampling plot (Villéger et al., 2008), we excluded from the ALL and UnderSt datasets all sampling plots with six or fewer species and 3471 plots remained for the analyses. For the OverSt dataset, the first two axes of the PCoA were maintained to avoid exclusion of plots with few phanerophyte taxa.

Finally, the FDis metric was calculated for the overstorey layer of 3270 plots, while the FRic metric was calculated for 2916 plots, respectively. Since taxa with higher abundances are expected to have a greater influence on the functional structure of the community (Májeková et al., 2016), abundance information was included for the calculation of the functional dispersion index after its square-root transformation. The metrics of multivariate functional diversity were calculated with the *dbFD* function of the FD package in R software (Laliberté et al., 2015; Laliberté and Legendre, 2010).

The standardized effect sizes (SES) of FRic and FDis were calculated to investigate the functional structure of community types. According to Götzenberger et al. (2016), null model selection can significantly affect the correct identification of assembly processes in a dataset. More specifically, when only environmental filtering or only limiting similarity processes affect community assembly, then a null model that maintains species frequency, total abundance and total species richness fixed is preferable (trial swap null model; Götzenberger et al. 2016). In contrast, when environmental filtering and limiting similarity simultaneously affect community assembly, a null model that maintains only the plot species richness and total sample abundance fixed is the most appropriate (richness null model) (Götzenberger et al., 2016). The main null model employed in the present study for the estimation of SES.FRic and SES.FDis was the richness model since we had no reason to believe that there are no simultaneous effects of environmental filtering and limiting similarity in the communities, as shown in some previous studies (Kang et al., 2017; McGill et al., 2006). Thus, the estimations of the SES values of the functional diversity metrics were computed by creating 999 random community data matrices from the regional species pool of the 923 taxa with the richness null model by employing the *randomizeMatrix* function of the picante package in R (Kembel et al., 2010). Subsequently, all indices were computed for the randomized communities, and the SES values were calculated as the observed FD relative to expected values from the random communities: SES = (observed FD index value − mean expected index value)/SD of the index across 999 randomizations. The table of plots × randomized functional diversity indices was used to calculate these SES values. The trial swap null model was also employed for comparison (Appendix C).

3. Results

Twenty-five floristically and ecologically well-differentiated community types were identified in the study area, grouped into four broad forest types. More specifically, the 3471 vegetation plots were classified in nine beech forest, three ravine forest, five pine forest and eight oak forest community types. A detailed description of these communities and a synoptic table presenting their floristic composition can be found in Mastrogianni et al. (2019): Supplementary Data 3 and 2, respectively.

3.1. *Patterns of functional identity*

Results derived from CWM and SES.CWM values based on the three datasets revealed partly different patterns between vegetation layers and forest types (Table 2). More statistically significant SES.CWM values were found for the ALL dataset, fewer statistically significant SES.CWM

Table 2

Contribution of each functional trait to the differentiation of forests types (B: beech, 9 community types; R: ravine, 3 types; P: pine, 5 types; O: oak, 8 types) according to the number of community types per forest type having CWM values significantly different from randomness based on the species richness (richness null model), for the UnderSt (understorey), OverSt (overstorey) and ALL datasets. The letters h or l within parentheses indicate if the community types are significantly higher or lower than under random expectation, respectively, in cases where more than 30% of plots of the community type had values statistically significantly different from the random expectations.

Traits	Categories of traits	CWMs UnderSt				CWMs OverSt				CWMs ALL			
		B	R	P	O	B	R	P	O	B	R	P	O
Beginning of flowering	autumn		3(h)					1(h)			3(h)	1(h)	
	early spring												
	spring												3(h)
	summer										2(l)		1(l)
Canopy height class										9(h)	3(h)	5(h)	8(h)
Canopy structure	regularly across the stem										2(h)	1(h)	4(h)
	rosette		1(h)										
	semi-rosette										3(l)		
	shoot scarcely foliated												
	tufted												
Dispersal mode	autochoric												
	hemerochoric									1(h)	2(h)		
	meteorochoric							1(h)		2(l)	2(l)		2(l)
	nautochoric						1(h)				1(h)		
	zoochoric												
	other												
Duration of flowering											3(l)		3(l)
Flowering colour	blue/violet/lilac												
	brown/green			2(h)	1(h)	9(h)				9(h)	3(h)	5(h)	8(h)
	purple/red/pink					1(h)							
	white	1(h)											
	yellow/orange												
	no flower	5(h)	3(h)	3(h)	2(h)					1(h)	2(h)		
Leaf length		2 (h)					1(h)		2(h)				
Leaf persistence	overwintering green			2(l)	1(h)							1(l)	1(h)
	persistent green			2(h)			1(h)	4(h)				4(h)	
	summer green				1(l)		1(l)	4(l)		1(h)	1(h)		2(h)
	spring												
	no leaves												
Leaf ratio		2(h)		2(h)			1(h)	5(h)		1(h)		2(h)	
Life form	chamaephyte	1(h)		3(h)								1(h)	
	geophyte	1(h)	3(h)										
	hemicryptophyte	1(h)			1(h)						2(l)		1(l)
	phanerophyte									8(h)	3(h)	5(h)	8(h)
	therophyte	3(l)	1(h)	4(l)	1(h), 2(l)						3(l)	4(l)	1(h), 2(l)
Life span	annual	9(l)	3(l)	4(l)	1(h), 3(l)						3(l)	4(l)	1(h), 2(l)
	biennial												
	perennial	4(h)	1(h)	4(h)	4(h), 1(l)						3(h)	4(h)	4(h)
Pollen vector	cleistogamy	7(h)	2(h)	1(h)	4(h)					1(h)			
	geitonogamy		1(h)										
	insects			1(l)		2(l)		4(l)	1(h)	4(l)	1(l)	4(l)	3(l)
	selfing										1(l)	1(l)	2(l)
	water	6(h)	3(h)	3(h)	5(h)					2(h)	3(h)	3(h)	1(h)
	wind	4(h)		5(h)	4(h)	2(h)	1(h)	4(h)	1(h)	9(h)	3(h)	5(h)	8(h)
Seed length									3(h)	5(h)	3(h)	2(h)	8(h)
Seed ratio							1(h)						
Seed weight									1(h)		2(h)		6(h)
Storage behaviour	Intermediate					9(h)	2(h)			9(h)	3(h)	2(h)	1(h)
	Orthodox					8(l)			2(l)	8(l)	2(l)		
	Recalcitrant								8(h)		2(h)	1(h)	8(h)

values for the OverSt dataset and an intermediate number for UnderSt. Specifically, for the ALL dataset, in 274 cases (combinations of a community type with a trait-category) out of the total 1250 cases (25 community types × 50 trait-categories), more than 30% of community types' plots were found with statistically significant SES.CWM value. The corresponding numbers for UnderSt and OverSt datasets were 131 and 84, respectively. In addition, significantly higher values (for numerical traits) or higher occurrence frequency of a trait category (for categorical traits) than expected by chance were more commonly observed than significantly lower values or lower occurrence frequency values for all datasets (369 cases for significantly higher values versus 120 cases for significantly lower values).

Statistically significant SES.CWM values were particularly frequent for ravine forests (40.7% of the 150 cases, i.e., 50 trait-categories × 3 ravine forest community types) for the ALL dataset, indicating their functional uniqueness among the studied forest community types, while statistically significant SES.CWM values were more frequent for pine forests for the UnderSt and OverSt datasets (14.4% and 9.2%, respectively). Investigation of functional identity with the ALL dataset revealed certain quantitative traits or categories of qualitative traits which were found with statistically significant SES.CWM values for all the studied community and forest types. These traits, including canopy height, brown/green flowering colour, phanerophyte life form and wind as a pollen vector, possibly characterize all the forest community types recorded in the study area.

Certain traits or their categories were found to be significantly different from randomness for a high proportion of community types within certain forest type(s) and simultaneously for a low or zero proportion of community types within the remaining forest type(s), thus differentiating functionally the former from the latter. For instance, the presence of autumn-flowering taxa is differentiating ravine forest types, leaf persistence throughout the year differentiates pine forest types, while a high presence of recalcitrant seeds differentiates oak forests (Table 2).

The results of the correlation among trait and trait categories with EIV are presented in Appendix E, Table E.2. From the 50 traits and trait categories investigated, 15 appeared to be correlated with many or few EIVs. From those, seven were traits and trait categories related to dispersal processes, four related to reproduction processes and four related to competitiveness and stress tolerance. The correlation among traits and the indicator of temperature was more commonly observed, compared to the rest of EIVs, while the indicator more rarely correlated with traits and trait categories was the reaction.

Differentiation patterns of the functional identity among community types were, to a large extent, similar across the three datasets, according to the NMDS. The results for the ALL dataset are presented here since they provide the best discrimination between the community types (Fig. 1), while the respective analysis for the OverSt and UnderSt datasets are in Appendix D. The stress value of NMDS analyses were 0.1360, 0.1128 and 0.1633 for the ALL, UnderSt and OverSt datasets respectively, indicating a good representation of data in the two-dimensional NMDS graphs. Regarding the ALL dataset, the forest types were discriminated in the NMDS diagram, indicating a clear differentiation of their functional composition. The first NMDS axis (NMDS 1) discriminated the pine forests from the broadleaved deciduous forests. At the same time, ravine forests were also discriminated from the other

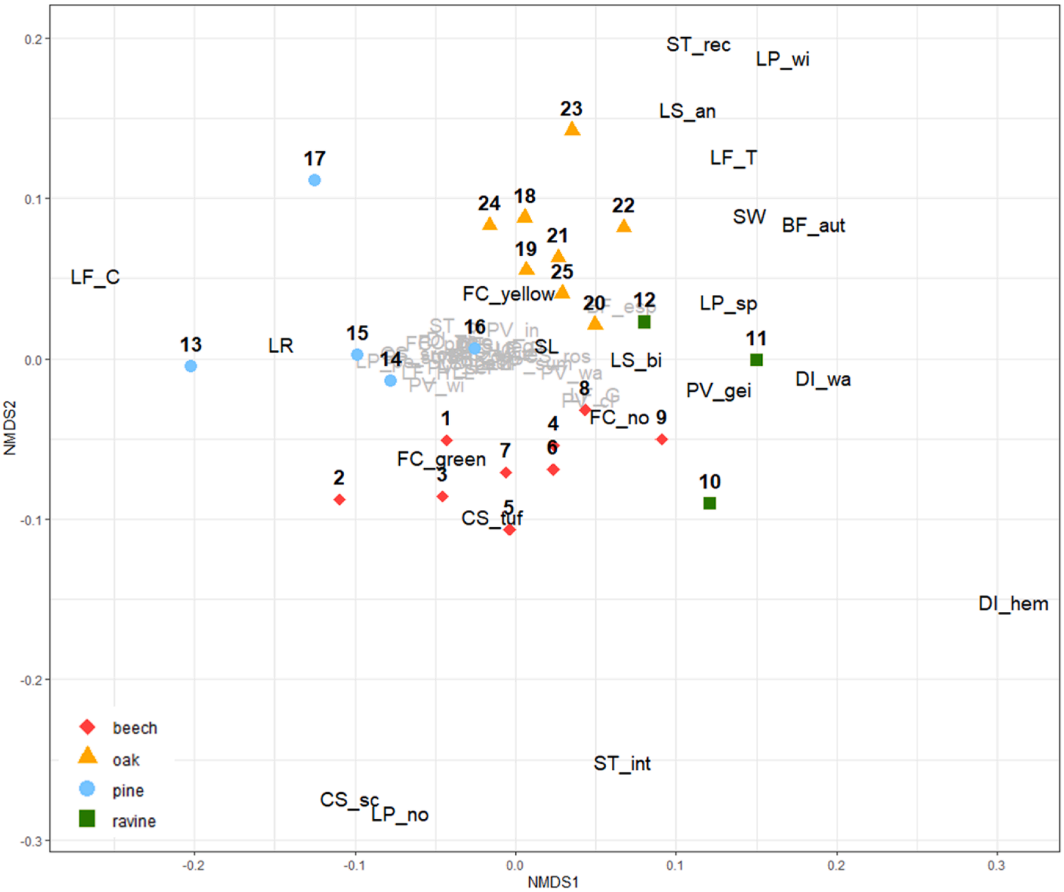

Fig. 1. Non-metric multidimensional scaling of the twenty-five forest community types (1–9: beech forests, 10–12: ravine forests, 13–17: pine forests, 18–25: oak forests) based on their Community Weighted Mean values and for the ALL dataset. Functional traits are represented by black (distinguishable) and grey (overlapping) letters. See Table 1 for abbreviations of functional traits. A magnified central part of the diagram (overlapping grey-coloured labels) is presented in Appendix D, Figure D.1.

deciduous forest types by appearing at the right part of the axis, indicating a distinct functional identity. The second NMDS axis (NMDS 2) separated mainly the oak from the beech forests. On the one hand, taxa with functional characteristics such as the beginning of flowering in summer (BF_sum), semi-rosette canopy structure (CS_sros), wind dispersal (DI_wi), leaf persistence (LP_per), more round leaves (LR) and chamaephyte life form (LF_C) were decreasing from pine to deciduous broadleaved forests. Taxa with leaves green in summer (LP_sum), geophytes (LF_G), geitonogamous (PV_gei) or with elongated seeds (LR) were following the opposite trend. On the other hand, the main differences in traits composition between oak and beech forest types concerned the most frequent presence of taxa with yellow/orange flowers (FC_yellow), overwintering green leaves (LP_wi) or orthodox (ST_or) or recalcitrant seeds (ST_rec) in oak forests, while taxa with scarcely foliated shoots (CS_sc), autochoric (DI_aut), with brown/green flower colour (FC_green), parasites (LP_no), pollinated by wind (PV_wi) or with intermediate seed storage behaviour (ST_int) were more frequent in beech forests.

3.2. Patterns of functional diversity

Regarding the results from all the multivariate metrics applied (FRic, SES.FRic, FDis and SES.FDis), the values of plots of the ALL dataset were correlated with the respective values of the UnderSt dataset. No other statistically significant correlations were found for the rest of the combinations of these metrics between ALL and OverSt or OverSt and UnderSt datasets. Moreover, none of the functional diversity metrics was highly correlated with the Ellenberg indicator values, which reflect the environmental conditions of the plots (Appendix E).

Patterns of differentiation of forest types based on FRic were similar between ALL and UnderSt datasets (higher FRic in oak forests and one pine community type) but differed for the OverSt dataset (higher FRic in ravine forests) (Appendix C, Figure C.1). Regarding functional dispersion, lower FDis values were observed for three pine community types in the ALL dataset, beech forests in the OverSt dataset, while higher levels of FDis were observed for ravine forests and some oak community types in the UnderSt dataset (Appendix C, Figure C.1).

Based on SES.FRic and SES.FDis, most of the community types did not differ statistically significantly from random expectations (Fig. 2). More functionally structured plots were identified for the SES.FDis metric and for all datasets, while few structured plots were found when SES.FRic was employed, and only for the OverSt dataset. In addition, the clustered structure was mainly found for the UnderSt dataset, while overdispersed patterns were identified for a few community types of the ALL and OverSt datasets (Fig. 2).

4. Discussion

We explored the patterns of functional diversity and identity among 25 broad-leaved and mountain coniferous forest community types at a regional scale (northern and central Greece). In addition, we compared these patterns between species with different life form that appear in different forest layers.

4.1. Functional identity differentiation between forest community types and forest layers

We found that the differentiation of forest types in species composition is well reflected in their functional composition. For many of the analyzed traits, community types were characterized by CWMs different from random expectations. The most significant differentiation was revealed when all the vascular plant taxa were included in the analysis (understorey and overstorey layers). In contrast to functional diversity, we did not find striking differences between the three datasets (ALL, UnderSt and OverSt) along to the main gradients revealed by the ordinations of CWM values of each community types (see Fig. 1 and Figs. D.1 to D.5). Specifically, the community types were similarly distributed in the NMDS diagrams derived from the three datasets, with the only exception of pine forests whose distribution partly differed for the OverSt compared to the other two datasets.

However, opposite patterns of correlations of some functional traits and trait categories with the NMDS axes (see Tables D.2 to D.4) were observed between UnderSt and OverSt datasets, such as “flowering in spring”, “flowering in summer”, “nautochoric dispersal mode”, “white flower colour”, “summer green leaf persistence”, “geitonogamy” and “intermediate storage behaviour”. These findings demonstrate that a separate investigation of the functional identity of different forest layers can provide complementary information regarding the functional characteristics of community types, as suggested in the literature (Lagerström et al., 2013; Luo et al., 2019a). This was also supported by the correlations of trait and trait categories with EIVs. Particularly, most cases of the correlation between traits and environmental gradients represented by EIVs were observed when only the understorey taxa were included in the analyses. The temperature was revealed to have the greatest effects on functional diversity in the studied community types, in agreement with several studies that have highlighted the significant effects of temperature on understorey composition and functioning (Maes et al. 2020, Lu et al. 2017, Moles et al. 2014).

Although the understanding of the functional identity of each community type is better when analyzing the forest layers separately (demonstrated by ses.CWM values), the discrimination of community types is better when the total floristic composition (ALL dataset) is employed (as demonstrated by the NMDS analyses). The traits that were found to have statistically significantly higher values (or higher occurrence frequencies for categorical traits) from random expectations for most of the 25 community types are indeed common traits for forest ecosystems. For example, wind-pollinated and green-flowering species (which have also been found to be associated with each other; Griffiths and Lawes, 2006) are known to characterize temperate forests (Binkenstein and Schaefer, 2015; Griffiths and Lawes, 2006). In addition, the statistically significantly higher values of characteristics such as seed length and canopy height partly results from the different life-history strategies of the tree versus herb species that are simultaneously occurring in forest ecosystems. It also explains the fact that these patterns are observed only when the ALL dataset is analyzed.

The traits found to differentiate certain forest types can indicate the underlying ecosystem processes shaping the investigated forest types. Beech, ravine, pine and oak forest types are clearly differentiated from each other through traits related to all three central processes involved in community assembly (reproduction, dispersal and competition). Flowering period and duration (reproduction traits) were found to differ as important functional traits based on which ravine and oak community types differed between each other as well as from the rest of the forest types. Furthermore, flower colour or the frequency of non-flowering plants differentiate beech, ravine and oak forests. Pine forests seem to differ from the other three forest types in terms of pollination vectors. Flowering phenology can influence species abundance and occurrence through competition effects (Sargent and Ackerly, 2008), and it reflects processes related to the availability of resources and their acquisition by plants (Craine et al., 2012). Oak and ravine forests were found to be dominated by larger- and heavier-seeded taxa and higher frequency of taxa with recalcitrant seeds. Each of these traits and trait categories was also found to be positively correlated with one of the environmental gradients of light, temperature and soil reaction, while a negative correlation was observed only between the occurrence of taxa with recalcitrant seeds and moisture availability. Seed characteristics and their storage capacity influence plant community structure, dynamics and succession (Vázquez-Yanes and Orozco-Segovia, 1996). They reflect several factors such as dispersal processes, plant responses to disturbances, soil resources and competition, and abiotic filters related to climate (Jiménez-Alfaro et al., 2016). Finally, vegetative and whole-plant traits, especially canopy structure, life form, life span and leaf

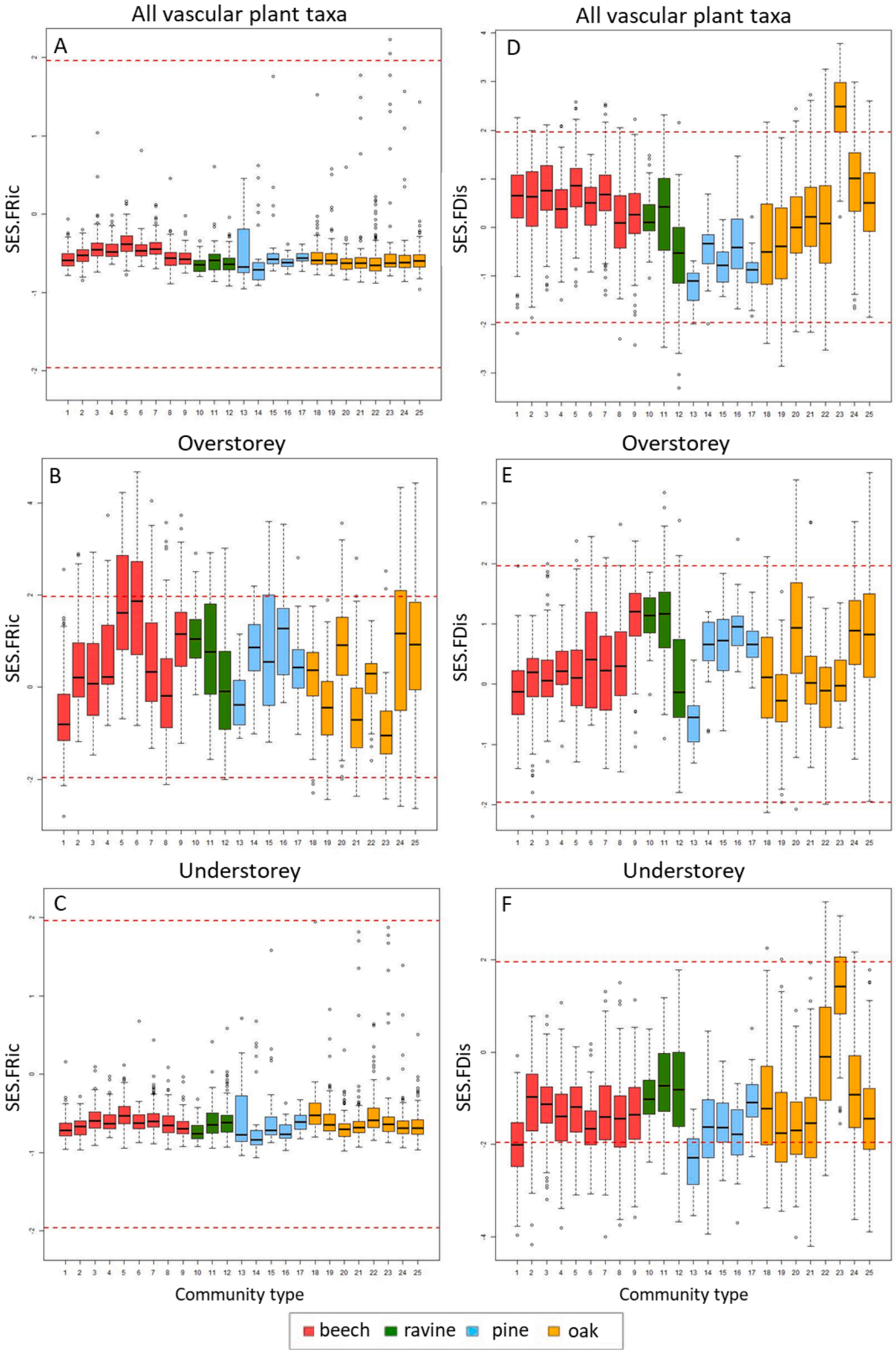

Fig. 2. Standardized effect sizes of functional diversity (SES.FRic; A, B, C) and functional dispersion (SES.FDis; D, E, F) in the 25 forest community types based on the “richness” null model for all vascular plant taxa (ALL dataset; A, D), only phanerophyte taxa (OverSt dataset; B, E) and taxa with life forms other than phanerophyte (UnderSt dataset; C,E). The box plots show medians, quartiles, 5–95-percentiles and extreme values. Values < -1.96 indicate significant functional clustering, whereas values greater than 1.96 indicate significant functional overdispersion. These threshold values are indicated by dashed red lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

persistence, contribute significantly to the differentiation of all forest types between each other. These traits are related to the competitiveness and stress tolerance of plant taxa (Grime et al., 1988). For instance, a higher occurrence frequency of the trait category “leaves distributed regularly along the stem” (CS_reg) for the ravine and oak forests reveals a higher competitive ability of the species they host (Barkman, 1988). The lower frequency of species with semi-rosette leaves in ravine forests indicates a lower frequency of less competitive species, and the opposite signal is derived from the higher frequency of evergreen species in pine forests (Roscher et al., 2012).

4.2. Functional diversity differentiation between forest community types and vegetation layers

In contrast to our expectations, we did not find significant evidence of differentiation among the 25 forest community types based on the functional diversity metrics applied here and the total floristic composition of plots (ALL dataset). Thus, in agreement with Spasojevic and Suding (2012), it is becoming apparent that single-trait metrics of functional diversity revealed more patterns of functional diversity than the multifacet approach. Nevertheless, in agreement with our expectation and recent research results (Lagerström et al., 2013; Luo et al., 2019a; Zhang et al., 2017), the patterns of functional diversity differed between the forest layers. Specifically, when one of the layers of a community type (either overstorey or understorey) was characterized by a statistically significant pattern, the other layer did not differ from randomness. This possibly indicates that different drivers of community assembly may affect the two forest layers, resulting in decoupled functional patterns of understorey and canopy species (Lagerström et al., 2013; Luo et al., 2019a).

Functional clustering was not observed for the overstorey layer of any community type. Considering the lack of correlation between functional diversity and the prevalent environmental conditions in the plots, we can assume that these functionally random or even overdispersed patterns result from the absence of strong environmental filtering in the study area.

The prevalence of clustered structure in several community types based on their understorey layer may be attributed to several factors. One candidate factor may be the effect of the distinct microhabitat conditions due to differences in canopy composition (Barbier et al., 2008) resulting in resource filtering (e.g. Cornwell and Ackerly, 2009; May et al., 2013). Zhang et al. (2017), in their conceptual diagram about biodiversity-ecosystem functioning relationship, show that both overstorey and understorey species diversity is affected by climatic and site conditions as well as successional stage, but understorey species are additionally affected by species diversity and biomass of the overstorey. Furthermore, species diversity and thus also functional trait diversity is expected to be much higher for understorey than for overstorey species. This higher diversity may be due to several reasons, such as the higher diversity of the understorey species in the regional species pool in comparison with that of the overstorey species, the smaller scale of habitats that the understorey species utilize in comparison with the overstorey species, or larger habitat heterogeneity for understorey species. Finally, it cannot be excluded that herbaceous and woody taxa are affected by environmental factors in different ways, also resulting in such contrasting patterns of functional diversity between these life forms (Lagerström et al., 2013; Luo et al., 2019a; Xu et al., 2018). However, it should be noted that our results showed a more frequent occurrence of significantly structured assemblages (specifically clustered) for the understorey layer in comparison with the overstorey layer, which contradicts the results of Luo et al. (2019b), who found more structured cases for the tree and shrub layers and random structure for the herbaceous layer.

The random structure of all the investigated community types when all the vascular plant taxa were included in the analysis is considered the outcome of such complex relations. Specifically, the multiple biotic and abiotic factors, including processes such as equalizing fitness or facilitation, can lead to the observation of random structure (Spasojevic and Suding, 2012).

4.3. Functional distinctiveness of community types

Among the four forest types, ravine forests appeared to be the most functionally distinct since they had by far the highest numbers of functional trait values that differed statistically significantly from random expectations (ses.CWM based on the ALL dataset). Besides ravine forests, pine forest seems to be also distinct in terms of their functional identity. These two forest types were at the edges of the NMDS ordination space of ALL and UnderSt datasets.

As mentioned above, for pine forests, this can be mainly attributed to the prevalence of more adverse environmental conditions. In contrast, the traits related to the functional distinctiveness of ravine forests are primarily indicative of the prevalence of biotic interactions (e.g., competition) between the taxa of ravine community types or the prevalence of distinct seed and dispersal-related functional characteristics.

Such prevalence of significantly large and heavy seeds and significantly low proportion of wind-dispersed taxa have been suggested to contribute to the unique functional signature of refugial areas (Keppel et al., 2018) since they are known to be associated with the generally more stable and favourable environment as well as more mesic conditions (such as north-facing slopes in the Northern Hemisphere) (Bhagwat and Willis, 2008; Copeland and Harrison, 2015; Kooyman et al., 2011). For most of the ravine forest community types, such characteristics were simultaneously observed for many taxa, constituting a supportive argument for their general refugial role, in agreement with the respective inferences that were made based on their phylogenetic diversity and structure in a previous study (Mastrogianni et al., 2019).

Thus, the results of the present study, and more specifically the overdispersed values or frequencies of specific traits or their categories, may reflect some effects of deep past conditions on the current trait composition of some of the studied community types. Bruelheide et al. (2018), who also studied single-trait metrics, suggested that the drivers of past trait evolution are also reflected in the composition of today’s plant communities. However, multivariate indices of functional diversity applied in our study did not reveal any community type with a significant number of overdispersed plots which would indicate imprints of deep past conditions in the assembly of current communities.

5. Conclusions

Our study revealed complex patterns of functional diversity and functional identity among 25 deciduous broad-leaved and mountain coniferous forest community types in northern and central Greece. Overall, the multivariate indices of functional diversity used in this study did not reveal significant differences in the functional structure of the studied community types, rendering almost all of them as randomly structured based on their total floristic composition. However, these indices revealed differences in functional structure between the canopy and the understorey layer. The single-trait approach based on SES. CWMs employed to capture functional identity allowed the identification of the main attributes of functional differentiation of the studied community types. It also provided useful information about the functional signature of each community type. We revealed decoupled pattern between two key functional aspects of a community, functional diversity and identity, suggesting their complementarity and highlighting the value of their simultaneous investigation. Finally, the single-trait approach suggested the effects of deep past conditions on the functional composition of certain community types, specifically of ravine forests. However, multivariate trait analysis did not infer any such effects.

CRediT authorship contribution statement

Anna Mastrogianni: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing - review & editing. **Milan Chytrý:** Writing - review & editing. **Athanasios S. Kallimanis:** Writing - review & editing. **Ioannis Tsiripidis:** Conceptualization, Data curation, Methodology, Writing - review & editing.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108229.

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