


ARTICLE

Imprints of land use history and disturbance regime in phylogenetic diversity of Mediterranean plant communities

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Abstract

Mediterranean landscapes were drastically affected by high levels of abandonment of agricultural and other land practices during the last century. These changes in land use can have significant effects on diversity patterns by altering disturbance and competition equilibria within plant communities at the landscape level. Particularly, such changes have been found to affect the patterns of phylogenetic diversity and structure by causing nonrandom losses of species through filtering effects and landscape homogenization. By investigating diversity patterns across a region submitted to high levels of land use changes, located in a (sub-) mountainous area of northwestern Greece (northern Pindus), we aimed at understanding the patterns of phylogenetic diversity and structure in relation to land abandonment and the subsequent recovery of natural vegetation. We sampled 250 vegetation plots equally divided in grasslands and forests, distributed across the different classes of land use occurring in the general study area based on the period since the last change in land use. Standardized metrics of Faith's phylogenetic diversity, mean phylogenetic distance, and mean nearest taxon distance were used to investigate phylogenetic diversity patterns across communities and different land-use regimes. A Principal Coordinates of Phylogenetic Structure analysis was employed to evaluate the variation in lineage composition among communities, and boosted regression trees were used to identify the relative influence of community differentiation (as captured by the classification of sampling plots in ecologically and floristically distinct vegetation communities), plant life strategies (competition, stress tolerance, and disturbance), and climatic, topographic, and soil variables on phylogenetic diversity metrics. Community differentiation was identified as the main driver of phylogenetic patterns. Additionally, phylogenetic diversity and structure were observed as having a statistically significantly negative correlation with disturbance, a statistically significantly positive correlation with stress tolerance, and a weaker positive correlation with competition. Phylogenetic clustering was observed for the early successional grassland

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communities submitted to stronger effects of disturbance, while phylogenetic randomness (or rarely overdispersion) was observed in forest communities submitted to stronger effects of competition. Finally, phylogenetic clustering of grassland communities was more evident shortly after land abandonment.

KEYWORDS

competition, disturbance, forest, grassland, land use change, phylogenetic diversity, phylogenetic structure, vegetation succession

INTRODUCTION

Anthropogenic land use changes and their subsequent impacts on landscape configuration and local habitat conditions are among the main drivers of diversity and composition changes, by affecting the regional patterns of plant species persistence (Dornelas et al., 2014). Mediterranean landscapes have been historically characterized by unfixed boundaries between farmlands, woodlands, and fallow lands due to traditional land use systems, constituting old fields as a key landscape element of dynamic equilibrium (Papanastasis, 2007). Throughout the 20th century, permanent abandonment of agricultural and other land-use practices has become increasingly common across the Mediterranean Basin (Sluiter & de Jong, 2007; Weissteiner et al., 2011), especially in upland areas (MacDonald et al., 2000), mainly due to biophysical challenges (e.g., soil erosion, climate) and socioeconomic factors (e.g., markets' globalization, rural population decline, shrinking farm incomes) (Oppermann et al., 2012; Papanastasis, 2007). Changes in the management regime of an area (e.g., cessation of agricultural activities on cropland and grasslands) are often followed by passive recovery of natural vegetation through secondary succession (Levers et al., 2018; MacDonald et al., 2000). This process can cause landscape homogenization, through the transition of abandoned arable land to woodland even within a time period of ~20 years (Prach et al., 2014).

The impact of land abandonment and the secondary vegetation succession it triggers on biodiversity have been mainly studied during the last two decades, with relevant studies mostly addressing species richness (SR), species distribution, and community composition issues (Queiroz et al., 2014; Subedi et al., 2022). However, understanding of diversity patterns, through the investigation of SR and composition during succession, can be complemented by investigating the evolutionary history of species in a community (Cadotte & Tucker, 2017; Forest et al., 2007). Phylogenetic diversity (PD) has been rarely assessed in relation to land abandonment (e.g., Belinchón et al., 2019; Deák et al., 2020; Turley & Brudvig, 2016; Uchida

et al., 2019), although the steep spatial and temporal gradients of succession, and changes in the landscape, abiotic factors, and disturbance regimes that are created after land abandonment may constitute precious natural experiments for the exploration of phylogenetic patterns at the community or landscape level in relation to the abovementioned gradients. Such natural experiments can be exploited by applying hypothesis testing or exploratory (hypothesis generating) approaches (Davies, 2021), and thus investigating phylogenetic patterns as a cause or as a result, according to the view of Gerhold et al. (2015). For example, changes in the frequency and intensity of land use (land abandonment or management intensification) have been found to affect patterns of PD and structure of plant communities by causing nonrandom losses of low-abundance species of high phylogenetic distinctiveness (Uchida et al., 2019).

During secondary succession, the relative importance of disturbance and competition effects is altering rapidly, and changes in habitat and land use are expected to drive nonrandom modifications in biodiversity among branches of a phylogenetic tree (Lososová et al., 2021; Mace et al., 2003). Therefore, case studies with actual data regarding processes such as disturbance and competition as well as PD across multiple habitats can be particularly informative about the underlying mechanisms of species' lineages local coexistence. More specifically, on the one hand, phylogenetic clustering is expected shortly after disturbance (early successional stages), due to habitat alteration and establishment of closely related taxa that confer a benefit in disturbed environments (Bernhardt-Römermann et al., 2011; Helmus et al., 2010; Purschke et al., 2013). On the other hand, phylogenetic overdispersion is expected with the increasing importance of competition during later successional stages (Bartish et al., 2016; Lososová et al., 2021; Purschke et al., 2013). Additionally, different types of disturbance, as well as time since last disturbance have been found to have distinct effects on the observed patterns of PD and structure (Belinchón et al., 2019; Zhang et al., 2014), and previous studies have revealed inconsistent patterns of phylogenetic structure after a disturbance. For example, phylogenetic clustering of disturbed sites was observed in an old field system

(Dinnage, 2009), phylogenetic overdispersion was found during tropical forest succession (Letcher, 2010), while PD patterns were not consistently affected by disturbances in other studies (Arroyo-Rodríguez et al., 2012).

Grime's CSR model of plant life strategies (Grime, 1974, 2001) constitutes a functional diversity approach which can provide insights on such patterns concerning the actual levels of disturbance, competition, and stress tolerance in plant communities, as well as succession and vegetation change. Specifically, Grime's model assumes that functional responses of plants vary across different intensities of stress and disturbance in a local site, and can be employed to identify the functional signature of species and communities along environmental gradients or stages of vegetation succession (Li & Shipley, 2017; Rosenfield et al., 2019; Zanzottera et al., 2020). According to the CSR model, stress (constraints on production) and disturbance (physical damage) act as restricting aspects of vegetation, reducing competition for resource acquisition among neighboring species (Grime, 1974) and the equilibrium between the three main aspects of stress, disturbance, and competition for each vegetation community can be depicted in a CSR ternary plot. Ecosystems of low stress and disturbance are expected to be inhabited by plants of high competitive ability and the vegetation communities observed in such ecosystems are expected to have higher values along the competition (C) axis of the CSR ternary plot. Habitats of high stress but low disturbance are dominated by stress-tolerators, and therefore, are expected to be near the vertex representing the stress-tolerating strategy in the CSR ternary plot. Finally, ruderals are more common in the opposite case of low stress but high disturbance (Grime, 1974); thus communities with high levels of disturbance are expected to be near the vertex representing the ruderal strategy in the CSR ternary plot. Therefore, investigating the patterns of plant life strategies in relation to the levels of PD and structure of communities can be a particularly promising approach which will allow better insights regarding the potential drivers of community assembly.

Nonetheless, interpretation of PD patterns cannot be accomplished when considering only processes related to present or recent past, since species pools of different vegetation communities are largely shaped by old evolutionary processes (Lososová et al., 2021; Ricklefs, 2004). Thus, the cause of the observed patterns in present-day communities may be the result of deep-past processes that are related to macroevolutionary diversification, idiosyncratic histories of biogeographic regions or habitats within regions, or trophic interactions (Gerhold et al., 2018). Such a driver of phylogenetic patterns in landscapes significantly affected by land abandonment may be considered as very possible as the latter affects the cover and

distribution of open habitats (e.g., seminatural grasslands) and forests. Indeed, Lososová et al. (2015, 2021) found that these two general vegetation types, namely grasslands and forests, are structured from species pools with different PD due to their different age.

Overall, investigation of PD and structure of plant communities submitted to different types of disturbance frequencies and intensities, as well as after different time periods since land abandonment can help understanding of the currently observed phylogenetic patterns. Here, we study these patterns among different vegetation communities, representing the major part of the successional gradient occurring in our study area. This ranges from pioneer herbaceous communities found on newly abandoned fields to forest communities at the final stage of succession, in accordance with the area's climate. Our study area is located in the (sub-) mountainous altitudinal zone of the Pindus Mountains in Greece, which may be considered as a typical (sub-)mountainous Mediterranean landscape that has rapidly changed during recent decades due to extensive abandonment of land uses (Kiziridis et al., 2022; Liarikas et al., 2012; Zomeni et al., 2008). Our general objective was to assess the impact of land abandonment on the PD and structure of the vascular flora of our study area, by exploring their patterns as a result of the successional stage of plant communities, their current environmental and ecological differentiation, as well as their historical legacies of stress and disturbance processes. Our specific aims were to: (1) investigate the differences in PD and structure among communities representing different successional stages, (2) search for any strong dependence of communities' PD and structure on environmental variables, as well as the CSR plant life strategies at the community level, and (3) test whether there are differences in the communities' PD and structure in relation to the time since the last change in a land cover category, and thus with the time passed since the establishment of a different land cover.

METHODS

Study area

The present study was conducted in the northwestern sub-mountainous region of the Pindus Mountains in Greece. This area was selected as a characteristic Mediterranean (sub-) mountainous area where extensive land use existed in the past (before World War II), but in which high levels of land use abandonment were reported for the general region afterward (Liarikas et al., 2012; Zomeni et al., 2008). We have studied the land cover changes in the study area and we found a

great reduction in farmlands from 30% of the total study area in 1945 to 3% in 2015, while for the same period, we observed a corresponding increase in forests from 22% to 63% of the area (Kiziridis et al., 2022). A total of five circular study sites, with a diameter of 6 km each and a total area of 141.4 km², were selected on the basis of a preliminary investigation of the observed changes in relation to land use. More specifically, all five circular study sites included the five land use types investigated in the present study, namely farmland, grassland, open-scrub, closed-scrub, and forest. Nevertheless, the trends (in terms of extent and pace) of land use changes along the 70-year study period differed between the five sites (Kiziridis et al., 2022). Furthermore, the sites differed in terms of topography and other environmental factors (see *Environmental data*). Therefore, the distinction of five study sites, instead of using one single region, allowed the investigation of diversity across a wider range of landscape characteristics such as altitude, soil, and climatic conditions.

Vegetation data and analyses

In each circular study site, 25 grassland or shrubland vegetation plots with an area of 50 m² (2.5 × 20 m), as well as 25 woodland vegetation plots with an area of 200 m² (10 × 20 m), were sampled, leading to a final dataset of 250 vegetation plots (125 grasslands or shrublands and 125 woodlands). Vegetation plots representative of all the different general habitat types occurring within the study area were sampled, with the distribution and number of plots per habitat type being proportional to the distribution and extent of each habitat type (Appendix S1: Figure S1). For each sampling plot, we recorded all the vascular plant taxa and their cover along the different forest strata (herb, shrub, and tree layer) using the 9-grade Braun-Blanquet scale (Braun-Blanquet, 1964; Podani, 2006; Westhoff & Van Der Maarel, 1978; Wilmanns, 1989). Additionally, exact coordinates, altitude, slope, and aspect were recorded for each vegetation plot. Finally, species nomenclature followed the Euro+Med PlantBase (Euro+Med 2006–2021). The sampled plots were distributed along altitudes ranging from 302 to 905 m and slopes from 0° to 39°.

The different vegetation communities occurring in our study area were identified by employing standardized procedures of vegetation classification (McCune & Grace, 2002). All the species with one or two occurrences in the dataset were excluded prior to classification. Raw abundance values were standardized using the Hellinger method, which standardizes abundance by site and then applies a square root transformation (Legendre & Gallagher, 2001). This transformation method was

preferred in order to better linearize the distances among the sampling plots by emphasizing changes in relative species abundances instead of absolute abundances. Subsequently, the data were classified using the Flexible beta clustering ($\beta = -0.25$) in combination with the Bray–Curtis similarity measure by the *agnes* function of the “cluster” package in R (Mächler et al., 2012). The latter classification approach was selected as the most appropriate to represent the floristic differentiation of the sampled vegetation plots, after conducting preliminary investigation of data classification by employing other distance and clustering methods commonly employed in the field of vegetation science (McCune & Grace, 2002).

In order to make sure that comparison of diversity levels among the different communities was fair, despite the number of vegetation plots classified in each community, their sample completeness was assessed by using the “iNEXT” package for R (Hsieh et al., 2016). For estimating environmental conditions of communities, we employed the ecological indicator values (EIV) for Europe for light, temperature, soil reaction, moisture, and nutrient availability (Dengler et al., 2023). We calculated the average indicator values for the 250 sampled plots, by using only taxa with three or more occurrences in the dataset, weighted by their abundance, raised to a power of 0.3 to reduce the effect of dominant species. Additionally, for the taxa not included in the dataset of EIVs for Europe, we determined such values by averaging the values of the five taxa with the highest fidelity with the above taxa (at least 20). Subsequently, the weighted average indicator values for each plot were calculated. Mean EIVs for all identified communities are provided in Appendix S1: Figure S2.

Plant life strategies

Plant functional strategies are categorized into 19 classes, including 3 primary (C, S, and R), 4 secondary (CS, CR, SR, and CSR), and 12 tertiary classes (C/CR, C/CS, C/CSR, CR/CSR, CS/CSR, R/CSR, S/CS, S/CSR, S/SR, SR/CSR, R/CR, and R/SR) (Grime, 1977; Hodgson et al., 1999). For the allocation of CSR scores in the 468 taxa found in the sampled vegetation plots, we conducted functional trait sampling during the vegetative period of 2021. We collected 5 ± 2 well-developed individuals of 408 taxa (87.2% of the 468 taxa found in all vegetation plots), and we measured their leaf area (LA; in square millimeters), leaf dry matter content (LDMC: leaf dry mass/water-saturated leaf mass; in milligrams per gram), and specific leaf area (SLA: leaf area/leaf dry mass; in square millimeters per milligram), following standard protocols (Pérez-Harguindeguy et al., 2013).

Subsequently, we allocated CSR scores for each species, by using the median trait values of all sampled individuals per taxon with the application of the “Stratify” method (Pierce et al., 2017). For 15 (3.1%) of the taxa that we were not able to sample, CSR scores from closely related taxa in our dataset were employed, while CSR scores for 34 (7.3%) taxa were retrieved from databases (Chytrý et al., 2021; Pierce et al., 2017). For the remaining 11 (2.4%) taxa, CSR scores were left as missing values. Community-weighted mean (CWM) values for C, S, and R scores were calculated for each vegetation plot using species’ CSR scores weighted by their relative abundance (Behroozian et al., 2020), by the *functcomp* function of the R package “FD” (Lavorel et al., 2008).

Mapping of land cover per plot

Information regarding the period since the last change in land use–land cover for each vegetation plot was obtained through mapping of land cover for four distinct periods, namely years 1945, 1970, 1996, and 2015. Specifically, for each of these years, each vegetation plot was assigned to one of five land type categories, namely farmland, grassland, open-scrub, closed-scrub, and forest, corresponding to areas with evidence of agricultural management practices for farmlands or occurrence of natural or seminatural vegetation with cover of trees and shrubs of 0%–10%, >10%–40%, >40%–70%, and >70%–100%, respectively, for the rest of the land cover categories. For further details on mapping methodology and data sources, please see Kiziridis et al. (2022).

After taking into account the sequence of land use categories of each vegetation plot during the four mapping periods, we categorized all plots in four classes of land use change. The aim of this categorization was to identify the period during which the process of succession had remained uninterrupted for each vegetation plot. Specifically, grasslands were classified according to their age as follows: new grasslands (plots covered by grassland in the 2015 map, but covered by farmland or forest in 1996), 19-year-old grasslands (plots covered by grassland since 1996), 45-year-old grasslands (plots covered by grassland since 1970), and >70-year-old grasslands (plots covered by grassland since 1945). Respectively, forest vegetation plots were respectively categorized as new forests, 19-year-old forests, 45-year-old forests, and >70-year-old forests.

Environmental data

For testing the effects of environmental factors on PD and structure across the studied grassland and forest

communities, we selected a set of climatic, topographic, and soil factors. Climatic variables included temperature seasonality (SD of mean monthly temperatures; in degrees Celsius) and precipitation seasonality (CV in monthly precipitation) from the CHELSAcruts dataset (Karger et al., 2017). These downscaled at a 25-m spatial resolution, after spatial interpolation of the original coarser meteorological rasters (Kiziridis et al., 2022). For topographic variables, slope and eastness were derived from the Copernicus Digital Elevation Model (EU-DEM v1.1), with a spatial resolution of 25 m, while the sum of total nitrogen at 15-cm depth was obtained from the SoilGrids 2.0 dataset as soil variable (N15; Poggio et al., 2021), with a spatial resolution of 250 m. The aforementioned environmental variables were selected from a greater set of variables after checking for collinearity (see Kiziridis et al., 2022).

Phylogenetic tree

We used the time-calibrated megaphylogeny for seed plants, GBOTB (Smith & Brown, 2018), as a backbone for the construction of the phylogenetic tree of all species occurring in the sampled vegetation plots. This megaphylogeny contains 74,533 vascular plant species and includes all plant families (Smith & Brown, 2018). Subsequently, the *V. PhyloMaker* function (Jin & Qian, 2019) was applied in R (R Core Team, 2022). Since the employed megaphylogeny only includes taxa in the species level, taxa identified at the subspecies level in our dataset were used to the species level as well. For cases that more than one subspecies of the same species had been recorded in the same plot, total percentage cover was calculated by merging the cover of each subspecies under the independence assumption (Tichý & Chytrý, 2006). All families and genera occurring in our dataset were present in the backbone tree, and in total, 73.2% of our species (486 species) were included in the megaphylogeny. The remaining 26.8% of the species (178 species) were added as polytomies to the middle point of the branch length of their respective genera (Qian & Jin, 2021). The latter approach was selected as the most appropriate, since calculation of community phylogenetic metrics based on such polytomies has been shown to provide strongly correlated results with fully resolved species-level phylogenies (Qian & Jin, 2021).

PD and composition

We used three metrics to quantify PD and structure of the sampled vegetation plots. PD was calculated by

Faith's PD, which is the sum of the total branch length of all taxa included in a community (Faith, 1992). Phylogenetic structure was investigated by mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD) (Cadotte et al., 2010; Helmus et al., 2007; Webb et al., 2002). MPD is sensitive to deep branching structure, and thus, is strongly affected by the presence of species belonging to old and distinct lineages co-occurring in the same community, while MNTD is more strongly influenced by recent speciation (Mazel et al., 2016). Because PD, MNTD, and the variance of MPD are correlated with SR (Miller et al., 2017), their standardized effect size versions were calculated (ses.PD, ses.MPD, and ses.MNTD). In specific, for each vegetation plot, 999 simulated assemblages were created by employing the "regional" null model (function *newRegionalNull*, R package "metricTester"; Miller et al., 2017). The "regional" null model creates randomized communities with maintained plot SR, and probabilities of occurrence of all species being proportional to their regional abundance in the original data matrix. This null model was selected as it has been reported to simultaneously provide very low Type I and Type II errors (Miller et al., 2017). The values of phylogenetic metrics for the 999 simulated assemblages were compared with the respective observed values for each vegetation plot, to obtain standardized effect sizes according to the expression $SES = [\text{observed} - \text{mean}(\text{null})]/SD \text{ of null}$. Original values of plots were considered statistically significant when their SES values were greater than 1.96 or lower than -1.96 , corresponding to the 95% confidence limits for a standard normal distribution (Carlucci et al., 2017; Dias et al., 2020; Soliveres et al., 2012). All PD metrics were calculated for presence-absence data, since higher levels of Type I errors have been reported for results based on abundance-weighted data (Miller et al., 2017). Finally, gymnosperms and ferns were excluded from all analyses because they are generating exceptionally long evolutionary branches in the phylogeny, since their evolutionary history differs from that of angiosperms (Kubota et al., 2018; Massante et al., 2019). Nevertheless, in order to be fully informed, we additionally conducted analyses based on abundance data, as well as by including gymnosperms and ferns. We considered the results based on presence-absence data of all the angiosperm plant taxa occurring in the vegetation plots as the most informative dataset, and were therefore used as the main results in the present study, while the results based on abundance data and including all vascular plant taxa are presented in Appendix S1: Figures S3–S5.

Statistical analyses

A one-way ANOVA and Tukey test were employed for finding the differences in PD metrics among the studied community types. More specifically, ANOVA was performed with the *aov* function of the "stats" package in R for testing the effect of community types and land use change on the levels of phylogenetic diversity metrics. Subsequently, Tukey test was performed with the *HSD.test* function of the "agricolae" package in R to reveal the statistically significant differences between the tested groups. Pearson's correlation coefficient was employed to test the statistical significance of a linear association between SR and PD, for all the vegetation plots simultaneously and for grassland and forest plots separately. We used the Principal Coordinates of Phylogenetic Structure analysis (PCPS; Duarte, 2011; Duarte et al., 2012) to evaluate the variation in lineage composition among vegetation plots, by applying principal coordinates analysis (Gower, 1966; Legendre & Legendre, 1998) to a matrix of phylogeny-weighted species composition of plots. This analysis allows the ordination of plots according to phylogenetic similarity while clades determining these similarities can be assessed through their association with the PCPS axes. The first PCPS (those with higher eigenvalues) capture phylogenetic gradients in basal branches, where there is more variation in the age of clades, while the PCPS with lower eigenvalues captures variations in more terminal branches of the phylogenetic tree. For the calculation of PCPS, we employed the *pcps* function of the R package "PCPS" (Debastiani & Duarte, 2014).

Furthermore, we used boosted regression trees (BRTs; Elith et al., 2008), implemented in the R package "gbm" to test for the relative influence of plant life strategies, environmental variables, and community differentiation on ses.PD, ses.MPD, and ses.MNTD. More specifically, community differentiation refers to the potential effects that the ecologically and floristically distinct vegetation communities may have on the PD metrics, due to inherent characteristics such as habitat age and habitat lineage-pools. Additionally, regarding environmental variables, we used the plant life strategies of C and R (S was excluded due to collinearity with R), temperature seasonality, precipitation seasonality, slope, eastness, and N15 as predictors of the phylogenetic structure metrics. BRTs were selected for exploring relations between phylogenetic metrics and environmental variables since they 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 modeling techniques (Elith et al., 2008), and tend to be robust to missing data and irrelevant input variables, while they are also relatively

easy to interpret and visualize (Elith et al., 2008; Hastie et al., 2009). The optimum number of regression trees was obtained using a 10-fold cross-validation procedure, and for each variable, we obtained its contribution score (in percentage) as a measure of its relative importance in BRT models. Pearson's correlation coefficient was used to quantify the relationships between the plot-level CSR life strategies and ses.PD, ses.MPD, and ses.MNTD.

RESULTS

Vegetation communities

Vegetation classification led to the distinction of 11 communities, namely six grassland and five forest communities (Table 1; Appendix S1: Table S1). These communities were clearly floristically and ecologically differentiated. Additionally, they constituted distinct successional stages due to differences in their management regime as well as the time since last disturbance (Mastrogrianni et al., 2023). The first two identified communities were seminatural grasslands with *Chrysopogon gryllus* or with *Phlomis fruticosa*, which, according to their plot-level EIVs, are both found in relatively poor soils with low moisture availability and high temperature levels, despite the great difference in their altitudinal distribution. These two communities are subject to frequent grazing and, in terms of their successional age, they are advanced

stable grassland communities. The third community, old fields with *Hordeum bulbosum*, was found in varying altitudes and differed from the previous two seminatural communities mainly due to its higher nutrient availability and lower soil pH. This community is submitted to occasional disturbance in the form of mowing and grazing. Hay meadows with *Alopecurus rendlei* were located in the lower altitudes within our study area, and differed from all other grassland communities due to their lower temperature and higher moisture and nutrient availability levels. Old fields with *H. bulbosum* and hay meadows with *A. rendlei* constitute early-stage community grasslands, due to regular mowing and/or grazing. These grasslands are submitted to annual disturbance of both intensive grazing and mowing. The fifth grassland community was wet meadows with *Cynosurus cristatus*, which was characterized by very similar conditions to those of old fields with *H. bulbosum*, differing only slightly with their temperature levels. In addition, wet meadows with *C. cristatus* were submitted to infrequent mowing disturbance, similarly to old fields with *H. bulbosum*, but were also to some extent grazed. This community constitutes grasslands of more advanced and still ongoing succession. *Pteridium aquilinum* stands were found in few locations across our study area, and were characterized by significantly lower soil pH levels. It is a successional retrogressive community that has occurred after forest destruction.

Differences regarding the environmental conditions were less prominent in the case of forest communities.

TABLE 1 Identified communities within the study area as resulting from vegetation classification and their distinction in two general vegetation types (grasslands/forests).

General vegetation type	Community	No. plots	No. taxa	SC (%)	No. taxa	C	S	R
Grasslands	1. Seminatural grasslands with <i>Chrysopogon gryllus</i>	19	322	93	322	16.9	51.7	31.4
	2. Seminatural grassland with <i>Phlomis fruticosa</i>	26	313	95	313	17	50.9	32.1
	3. Old fields with <i>Hordeum bulbosum</i>	54	363	97	363	19	42.1	38.9
	4. Hay meadows with <i>Alopecurus rendlei</i>	10	122	77	122	18.2	42.9	38.9
	5. Wet meadows with <i>Cynosurus cristatus</i>	12	194	90	194	17.4	47.3	35.2
	6. <i>Pteridium aquilinum</i> stands	4	112	83	112	24.2	43.1	32.7
Forests	7. <i>Quercus frainetto</i> forests	33	180	96	180	29.7	42	28.3
	8. <i>Carpinus orientalis</i> forests	50	166	97	166	25.4	53.9	20.6
	9. Xero-thermophytic oak forests (<i>Quercus pubescens</i> – <i>Quercus trojana</i>)	17	184	89	184	24.9	54.2	20.9
	10. <i>Quercus cerris</i> – <i>Q. frainetto</i> mixed forests	21	177	90	177	29.7	46.3	24
	11. Riparian forests	4	68	74	68	35.8	41.1	23.1

Note: For each community, we present the number of sampled vegetation plots (No. plots), the number of taxa found within their plots (No. taxa), and their sample completeness SC (in percentage). The average community-weighted mean value of the three dimensions of the CSR model (competition, stress tolerance, ruderals) is presented for each community.

Particularly, *Quercus frainetto* forests were distinguished from the rest of the forest communities, due to their higher moisture availability and lower temperature. *Quercus cerris*–*Q. frainetto* mixed forests had intermediate levels of temperature and moisture availability compared with the rest of the forest communities, while *Carpinus orientalis* forests and xero-thermophytic oak forests (*Quercus pubescens*–*Quercus trojana*) had the lowest moisture availability and higher temperature among all forest communities. Finally, riparian forests were particularly different from the rest of the forest communities by having the highest levels of moisture and nutrient availability and lowest temperature levels. Regarding disturbance regime, forests in our study area are rarely or occasionally grazed, and selective logging is applied to them. In terms of succession, *C. orientalis* forests and xero-thermophytic oak forests (*Q. pubescens*–*Q. trojana*) are advanced but stable forest communities due to the effect of animal husbandry as well as past land uses. Finally, *Q. frainetto* forests, *Q. cerris*–*Q. frainetto* mixed forests, and riparian forests are late forest communities.

Differences in the number of sampled plots among communities resulted from the difference in their relative occurrence frequency within the study area. For eight communities, sample completeness was close to or higher than 90%, indicating a good representation of their diversity in the study area from the available sample plots. For the remaining three communities, sample completeness was not as high, but still higher than 74% in all cases. Due to the low number of vegetation plots of *P. aquilinum* stands and riparian forests, these two communities will not be particularly discussed.

Regarding the CSR functional strategy types, forest communities were found to have taxa with overall greater competitive ability than taxa found in grasslands (Table 1, Figure 1). The more mesic communities of *Q. frainetto* forests, *Q. cerris*–*Q. frainetto* mixed forests, and riparian forests were the ones with the highest levels of competitive functional strategy. The two remaining forest communities, namely *C. orientalis* forests and xero-thermophytic oak forests (*Q. pubescens*–*Q. trojana*), were distinguished from the rest of the forest communities

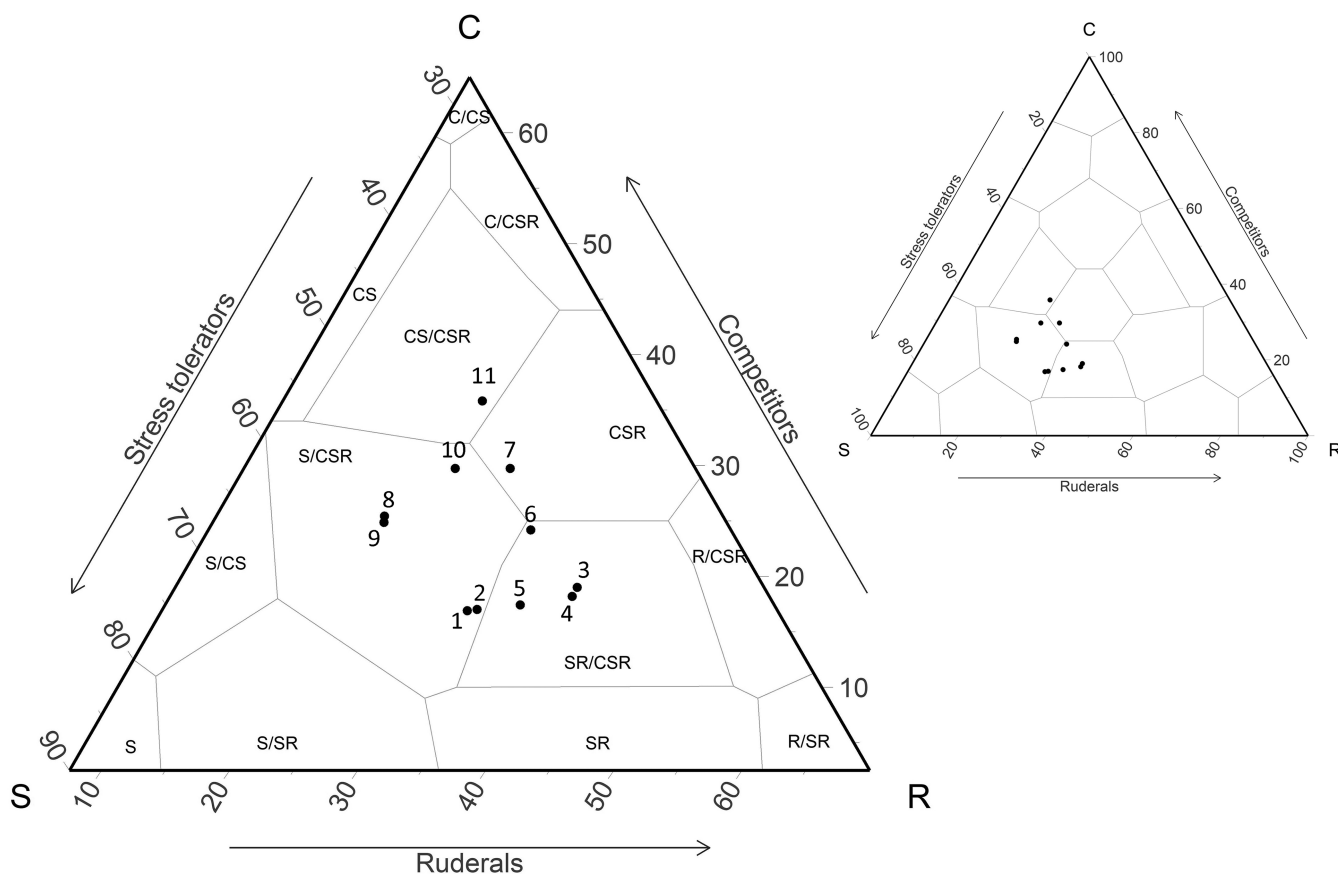


FIGURE 1 Close-up view of the distribution of the community-weighted mean competition–stress tolerance–ruderals (CSR) scores of the different communities, in the ternary plot (i.e., CSR triangle). C, S, and R represent the components of competitive, stress tolerating, and ruderal functional strategies in the CSR triangle, respectively. The coding of communities (1–11) corresponds to the numbering of communities presented in Table 1.

due to the high occurrence of stress tolerating taxa. Regarding grassland communities, the two seminatural communities were differentiated due to high occurrence of stress tolerators, while the rest of the main grassland communities (old fields with *H. bulbosum*, hay meadows with *A. rendlei*, and wet meadows with *C. cristatus*) had high occurrence of ruderal taxa, indicating that these communities are more intensively submitted to disturbances.

PD and composition of communities

According to the ANOVA, all the employed PD metrics differed statistically significantly among the community types ($p < 0.0001$). Based on Faith's PD and Tukey test (Figure 2), all grassland communities except hay meadows with *A. rendlei* had higher PD than forest communities (median value of grasslands' PD 1.27 times higher than median forests' PD), with seminatural grasslands with *C. gryllus* and *P. fruticosa* being the communities with the highest PD (median value of PD of these community types 1.31 times higher than the median PD of the rest of the grassland community types, and 1.52 times higher than the median of the forests' PD). PD was found highly and statistically significantly correlated with SR, for the set of all the vegetation plots ($R = 0.88$, $p < 0.0001$), as well as for the sets of grasslands ($R = 0.93$, $p < 0.0001$) and forests ($R = 0.9$, $p < 0.0001$), separately (Appendix S1: Figure S3). After standardizing for SR (ses.PD), the diversity pattern is reversed, with forests having higher PD than expected for their SR compared with grasslands (median values of forests' ses.PD was 3.36 SDs higher than grasslands' ses.PD). Particularly, old fields with *H. bulbosum*, hay meadows with *A. rendlei*, and wet meadows with *C. cristatus* had significantly lower PD than expected for their SR, while *C. orientalis* forests and *Q. cerris*-*Q. frainetto* mixed forests had significantly higher PD than expected for their SR. Regarding phylogenetic structure, old fields with *H. bulbosum* (based on ses.MPD and ses.MNTD), hay meadows with *A. rendlei* (based on ses.MPD), and wet meadows with *C. cristatus* (based on ses.MNTD) were found to be phylogenetically clustered. In contrast, forest communities were not found to be phylogenetically structured, except riparian forests that were found overdispersed. Results based on the abundance-weighted data, as well as on data with all vascular plant taxa (including gymnosperms and ferns), were very similar to those described above with few exceptions (Appendix S1: Figures S4–S6). For example, based on the presence-absence dataset with all vascular taxa and the ses.MPD metric, no grassland community was found to be clustered, while two forest communities

were overdispersed. Based on the abundance weighted dataset with all vascular plant taxa and the ses.MNTD metric, all communities were found randomly structured, except the *P. aquilinum* community, which was found again clearly overdispersed.

The first two axes of the PCPS analysis captured 35% of the total variance (Figure 3). Forest communities were clearly separated from grasslands and were characterized by their association with a great number of plant orders, indicating greater PD in basal branches. Differentiation among forest communities was not very clear. Oppositely, differentiation among grassland communities was high, with the exception of old fields with *H. bulbosum*.

Influence of environmental variables and CSR strategies on PD patterns

The greatest percentage of variation observed in the three standardized diversity metrics employed in the present study, as identified by the BRT method, was explained by three main variables (Figure 4). The community type was found to be the first and most important variable explaining variability of PD. Disturbance (R functional strategy) was found to be the second most important variable, with phylogenetic clustering occurring at vegetation plots with high levels of disturbance, and phylogenetic overdispersion being observed in plots with low level of disturbance (Figure 5, Table 2). Finally, competition (C functional strategy) was the third most important variable explaining PD, but with significantly lower relevant influence than community differentiation and disturbance (R functional strategy). Regarding the relation of competition with PD, phylogenetic clustering was observed at low levels of competition, and phylogenetic overdispersion at high levels of competition (Figure 5). The relative influence of the environmental variables, investigated in the present study, on the PD and structure patterns was significantly lower. More specifically, the variables of precipitation and temperature seasonality, slope, eastness, and soil nitrogen content at 15 cm depth had a cumulative relative influence on the phylogenetic metrics that did not exceed 27% of the total explained variance (Figure 4). The mean absolute errors of the BRT model built for the ses.PD, ses.MPD, and ses.MNTD metrics were 0.6, 0.42, and 0.56, respectively.

PD and time since last land use change

Communities were not found to be directly associated with a specific class of land use change since vegetation plots with at least three different classes of land use

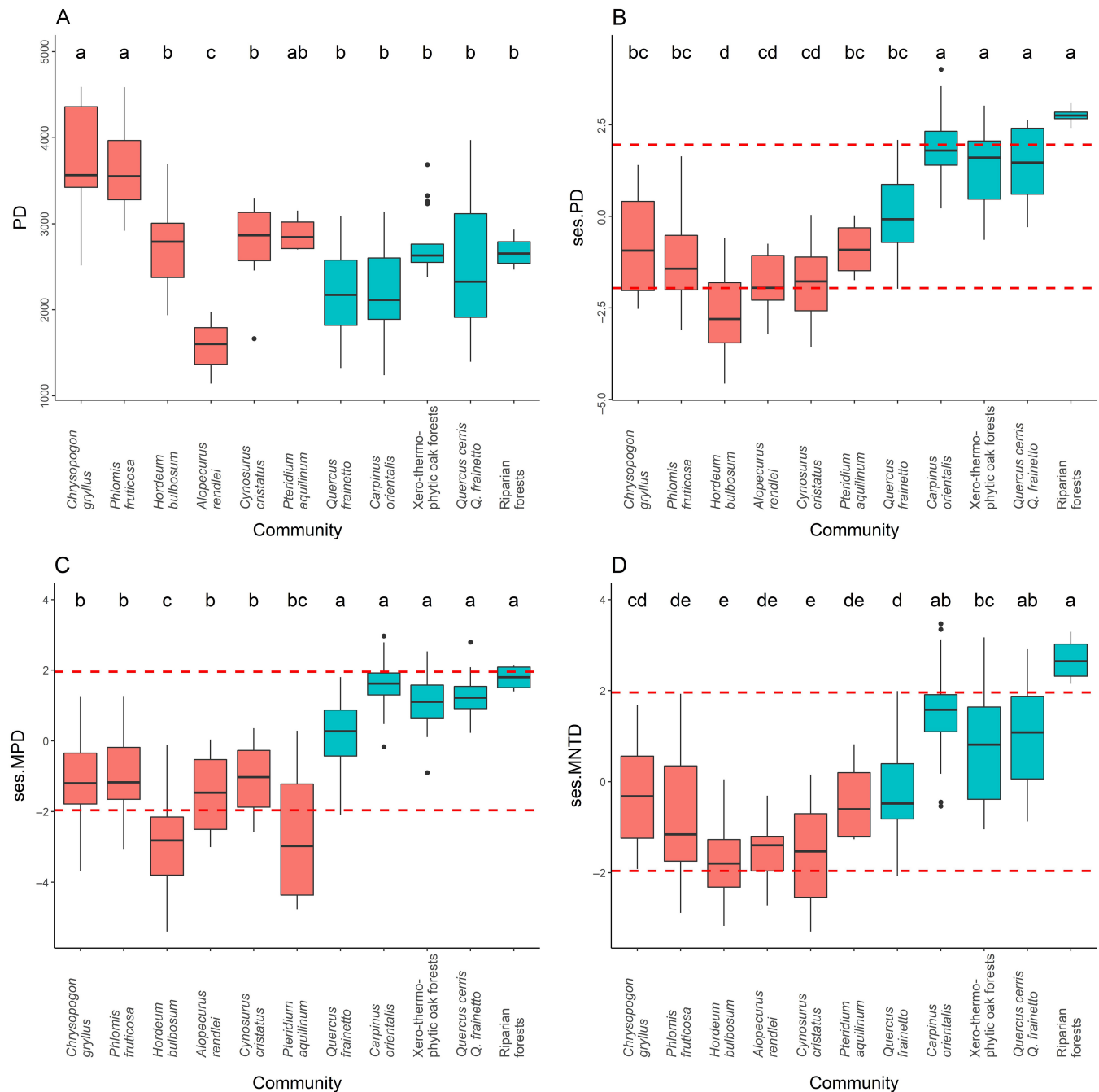


FIGURE 2 (A) Faith's phylogenetic diversity (PD) in the 11 communities. (B) Standardized effect sizes of Faith's PD (ses.PD). (C) Standardized effect sizes of the mean phylogenetic distance (ses.MPD). (D) Standardized effect sizes of mean nearest taxon distance (ses.MNTD) between taxa. All metrics have been calculated based on angiosperm taxa recorded in the sampled plots. Values < -1.96 indicate significant phylogenetic clustering, whereas values > 1.96 indicate significant phylogenetic overdispersion (according to the "richness" null model). The threshold values are indicated by dashed lines. The boxplots show medians, quartiles, 5–95 percentiles, and extreme values. Lowercase letters above boxplots represent ANOVA and post hoc Tukey test results. Red boxes represent grassland communities while blue boxes represent forest communities.

change were found in most communities (Appendix S1: Figure S6). An exception to this pattern was the case of seminatural grasslands with *P. fruticosa*, which were all located in areas where no land use change was mapped since 1945 (>70-year-old grasslands). According to the

ANOVA, all the employed PD metrics differed statistically significantly among the classes of land use change for the grasslands ($p < 0.0001$), similarly with the case of community types. Grasslands under longer uninterrupted succession (>70-year-old grasslands) were found to have

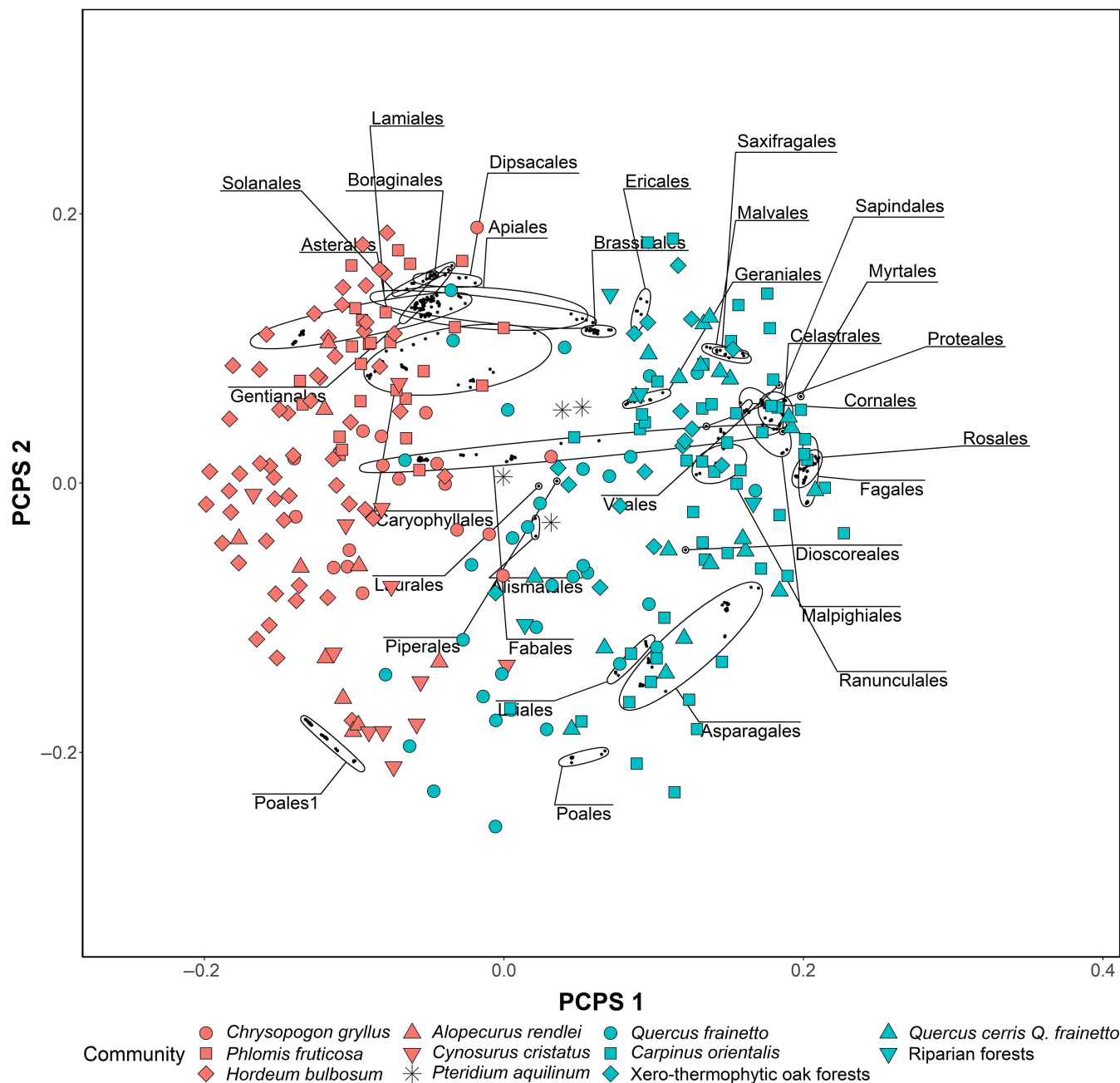


FIGURE 3 Scatter diagram showing the Principal Coordinates of Phylogenetic Structure (PCPS) scores for communities and plant species. Species are represented by small black circles, and ellipses represent groups of species belonging to the same plant order. Vegetation plots are represented by red and blue color for grasslands and forests, respectively. Vegetation communities are shape-coded, while the transitional pteridophyte community is depicted by black stars.

higher PD than more recently disturbed grasslands (new grasslands) (median value of PD of >70-year-old grasslands 1.32 times higher than the median PD of new grasslands) (Figure 6). This pattern was also maintained after standardizing for SR (ses.PD) (median values of >70-year-old grasslands' ses.PD was 1.11 SDs higher than new grasslands' ses.PD) (Figure 6). Additionally, the three first classes of land use change had statistically significantly lower PD than the one

expected based on their SR, while only the >70-year-old grasslands were found to have random levels of PD. For forest communities, most vegetation plots had random levels of PD, while small percentages of new forests and 19-year-old forests had statistically significantly higher PD than the one expected based on their SR. Regarding functional structure, new, 19-year-old, and 45-year-old grasslands were phylogenetically clustered based on both ses.MPD and ses.MNTD (except 19-year-old grasslands based

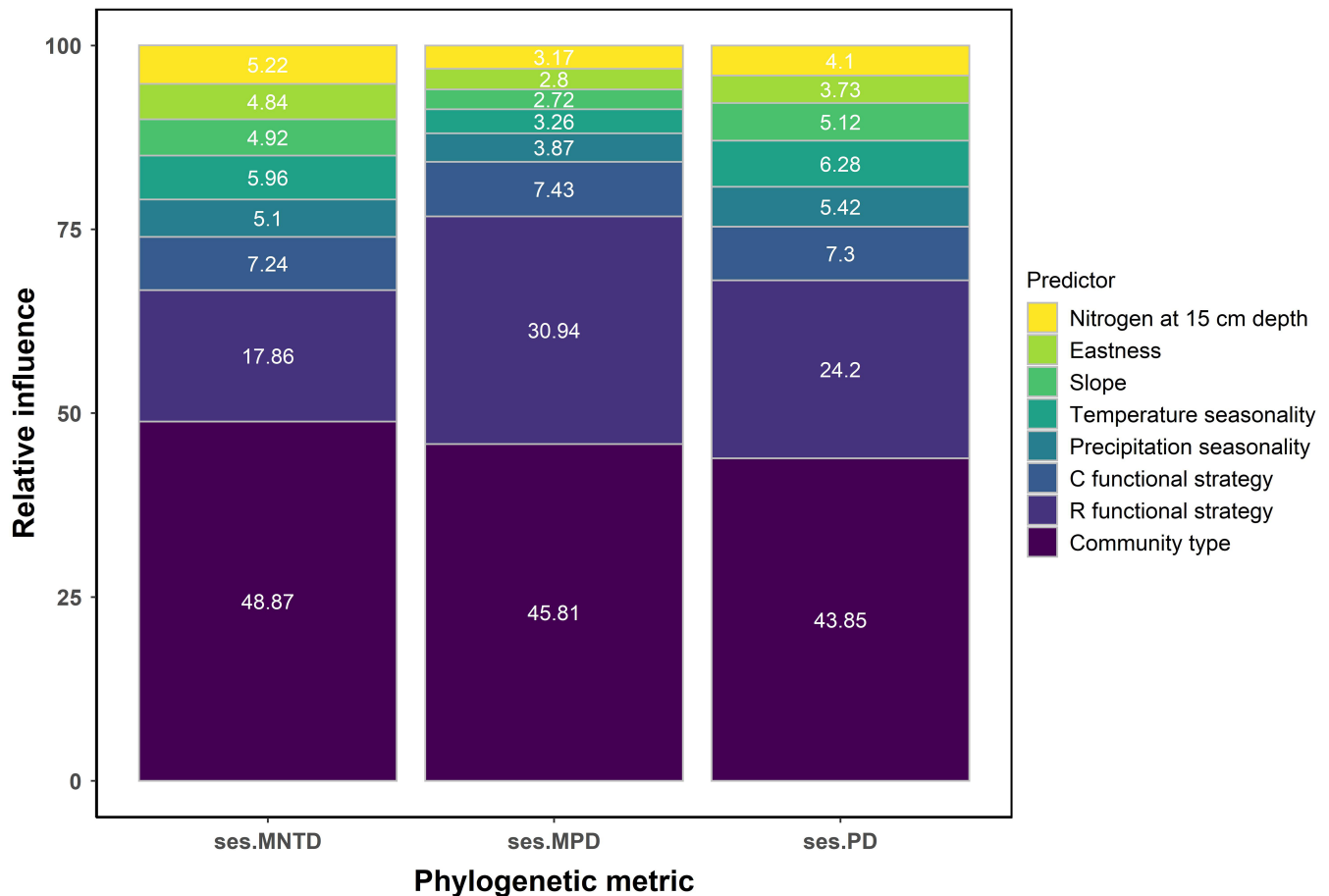


FIGURE 4 Relative influence (expressed in percentage) of vegetation community type, disturbance (R functional strategy), competition (C functional strategy), and environmental variables on standardized effect sizes of Faith's phylogenetic diversity (ses.PD), standardized effect sizes of the mean phylogenetic distance (ses.MPD), and standardized effect sizes of mean nearest taxon distance (ses.MNTD) values of the sampled vegetation plots.

on ses.MNTD). For both metrics, >70-year-old grasslands had a random phylogenetic structure similar to the case of forest vegetation plots of all classes of land use change. Nevertheless, the classes of land use change were not significantly differentiated from each other based on the PCPS analysis, neither for grassland nor for forest communities (Appendix S1: Figure S7).

DISCUSSION

We investigated PD and structure patterns among different plant communities occurring in a (sub-)mountainous landscape, and submitted to different levels of land use changes during recent decades. These communities represent the whole length of the successional gradient occurring in the study area. Although grassland communities were initially found to be phylogenetically richer than forest communities, this was found to be the result of richness dependence and the diversity pattern was

reversed after standardizing for SR. A high percentage of grassland vegetation plots was found to be phylogenetically clustered while phylogenetic randomness or, to a lesser extent, overdispersion was identified for forest vegetation plots. Additionally, plant community, disturbance, and competition were found to better explain the variation of PD and structure, while environmental factors were of lower importance. Following the recommendations of Gerhold et al. (2015), we interpret the observed phylogenetic patterns mainly as evidence of historical processes of distant or more recent past, instead of as proxies for community assembly mechanisms.

Effects of community differentiation on PD patterns

Community differentiation was found to be the main explanatory variable of PD within our study area. Overall, grassland communities, and especially the more

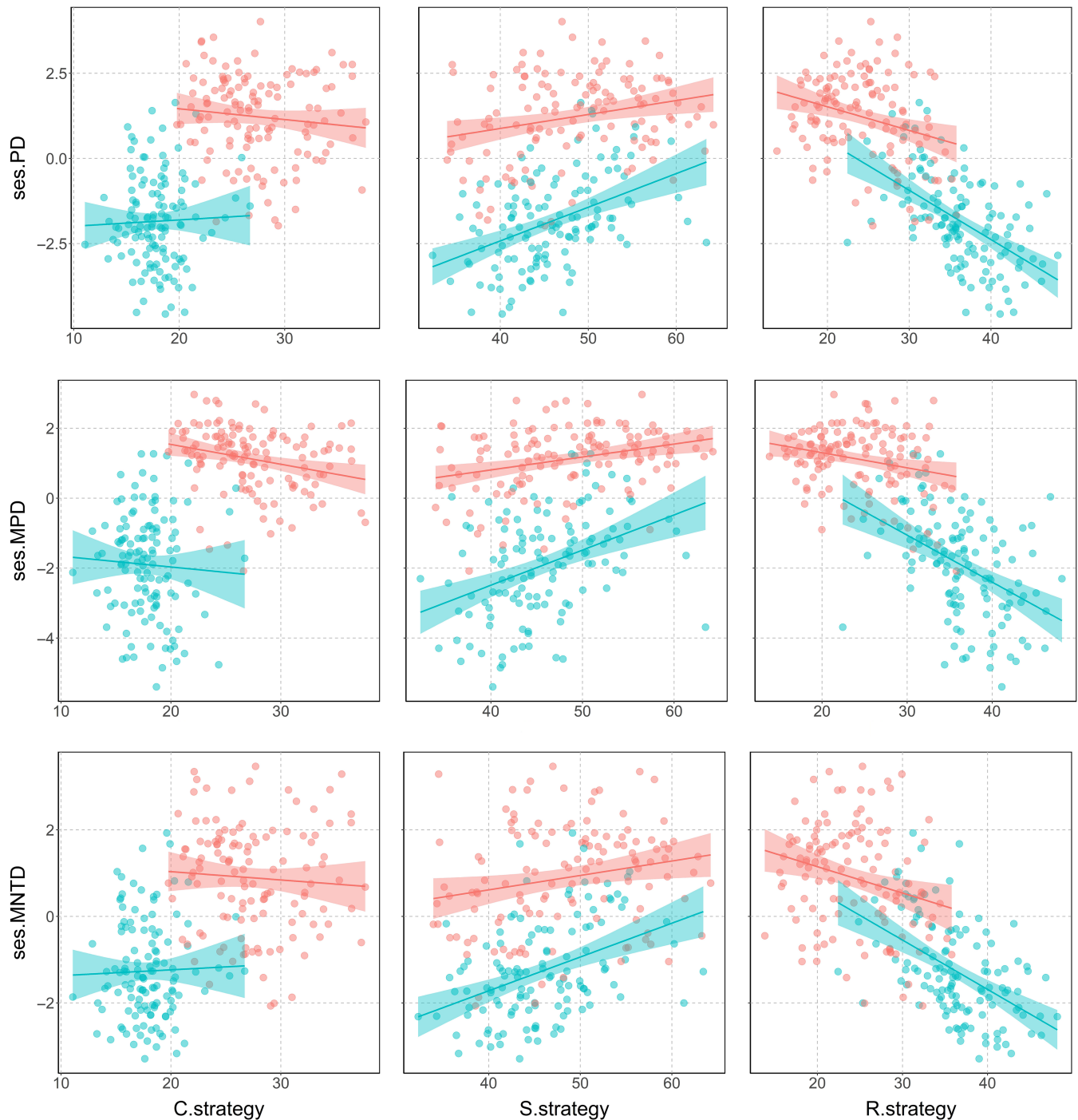


FIGURE 5 Correlations (colored lines) and CIs (shaded areas) among the competition (C), stress tolerance (S), and ruderal (R) life strategies, and standardized effect sizes of phylogenetic diversity (ses.PD), standardized effect sizes of Faith's mean phylogenetic distance (ses.MPD), and standardized effect sizes of Faith's phylogenetic diversity (ses.MNTD), for grassland (red) and forest (blue) vegetation plots separately.

successionally advanced ones, had statistically significantly higher SR than forest communities, with the exception of the early successional hay meadows with *A. rendlei*. Grasslands are generally known to harbor great levels of species diversity, despite their relatively recent origin, which dates about 70 million years ago and

is marked by the diversification of grasses (Petermann & Buzhdygan, 2021). High heterogeneity of microtopography and resources, biotic interactions, and anthropogenic disturbances are considered the main promoting mechanisms of SR in grasslands (Petermann & Buzhdygan, 2021). These SR patterns were consistent also

TABLE 2 Pearson's correlation coefficients among the metrics of phylogenetic diversity (PD) and structure (standardized effect sizes of Faith's PD [ses.PD], standardized effect sizes of the mean phylogenetic distance [ses.MPD], and standardized effect sizes of mean nearest taxon distance [ses.MNTD]) and the plot-level CSR (competition, stress tolerance, ruderals) values.

Plant life strategy	Dataset	ses.PD	ses.MPD	ses.MNTD
Competition	Overall	0.597***	0.570***	0.527***
	Forest	-0.107	-0.257**	-0.065
	Grassland	0.035	-0.052	0.030
Stress tolerance	Overall	0.347***	0.348***	0.331***
	Forest	0.248**	0.302***	0.203*
	Grassland	0.434***	0.395***	0.405***
Ruderals	Overall	-0.755***	-0.736***	-0.688***
	Forest	-0.281**	-0.237**	-0.249**
	Grassland	-0.534***	-0.444***	-0.497***

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

for the PD levels among the investigated communities, largely driven by the high statistically significant correlation observed between the PD and SR metrics in our dataset. This is the most commonly observed relationship observed between these two metrics (Tucker & Cadotte, 2013). PD has valuable applications in conservation decision-making (Faith, 1992) as a complementary surrogate for areas' prioritization (Cardillo, 2023; Forest et al., 2007), since it reflects the total evolutionary history of a species pool (Faith, 1994; Tucker et al., 2017). Standardization of PD for SR, that is calculation of ses.PD, led to the reversal of the ordering of communities, and showed that forest communities host more PD than grasslands. Investigation of the ses.PD patterns instead of the unstandardized ones constitutes a common practice that allows comparisons of PD between sets of species (e.g., assemblages, regions) (Tucker et al., 2017). The different age of the species pools of grasslands and forests in combination with their different SR patterns are the main reasons for the reversed ordering of communities based on PD and ses.PD values. Specifically, the higher SR of open habitats but their younger age, and the lower SR of forests but their older age is what drives the abovementioned reversal. Although for conservation purposes Cardillo (2023) leaves open the question whether regions with higher PD relative to SR should be prioritized against regions with higher total PD, for explorative or explanatory investigation of PD patterns we consider that the application of standardized PD values is more appropriate and avoids unveiling of patterns closely related to SR.

Additionally, based on ses.MPD and ses.MNTD metrics, phylogenetic clustering was observed for several grassland vegetation plots, while phylogenetic overdispersion and random dispersion were observed for forest vegetation plots (Appendix S1: Figure S8). Our results

fit with those of Lososová et al. (2021), who found strong phylogenetic differences between vegetation types of Europe. Also, Bartish et al. (2016) found, studying the phylogenetic structure of the vegetation types of the Netherlands, that vegetation types at the regional scale are assembled from different species pools according to their environmental conditions, that may have different heritage from different geological time periods. Specifically, the deciduous forests of *Quercetea pubescentis*, in which all the forest communities of our study area except the riparian forests belong to, were found as overdispersed by Lososová et al. (2021). They attributed this fact to the rich flora of these forests favored by a long-term persistence of favorable environmental conditions, the diversification of their flora for a long time and the long-term dispersal of species within deciduous forests. Phylogenetic overdispersion was found by Lososová et al. (2021) also for the forest of *Alno-glutinosae-Populetea albae* in which the riparian forests of the study area belong to. On the other hand, Lososová et al. (2021) reported clustered phylogenetic patterns for the grassland classes from which the grassland communities of our study area have many indicator species (e.g., *Stipo-Trachynietea distachyae*, *Festuco-Brometea* and *Chenopodietea*, *Moilinio-Arrhenetheretea*, and some classes of ruderal vegetation). Open human-made grassland habitats are considered significantly younger than forests (Strömberg, 2011), and therefore with significantly less time available for evolution and diversification of the lineages adapted to these habitats (Gerhold et al., 2008, 2015; Lososová et al., 2015). This is in agreement with our findings derived from the PCPS analysis, since all forest communities were clearly differentiated from grassland communities, due to the occurrence of significantly higher number of plant orders in forests.

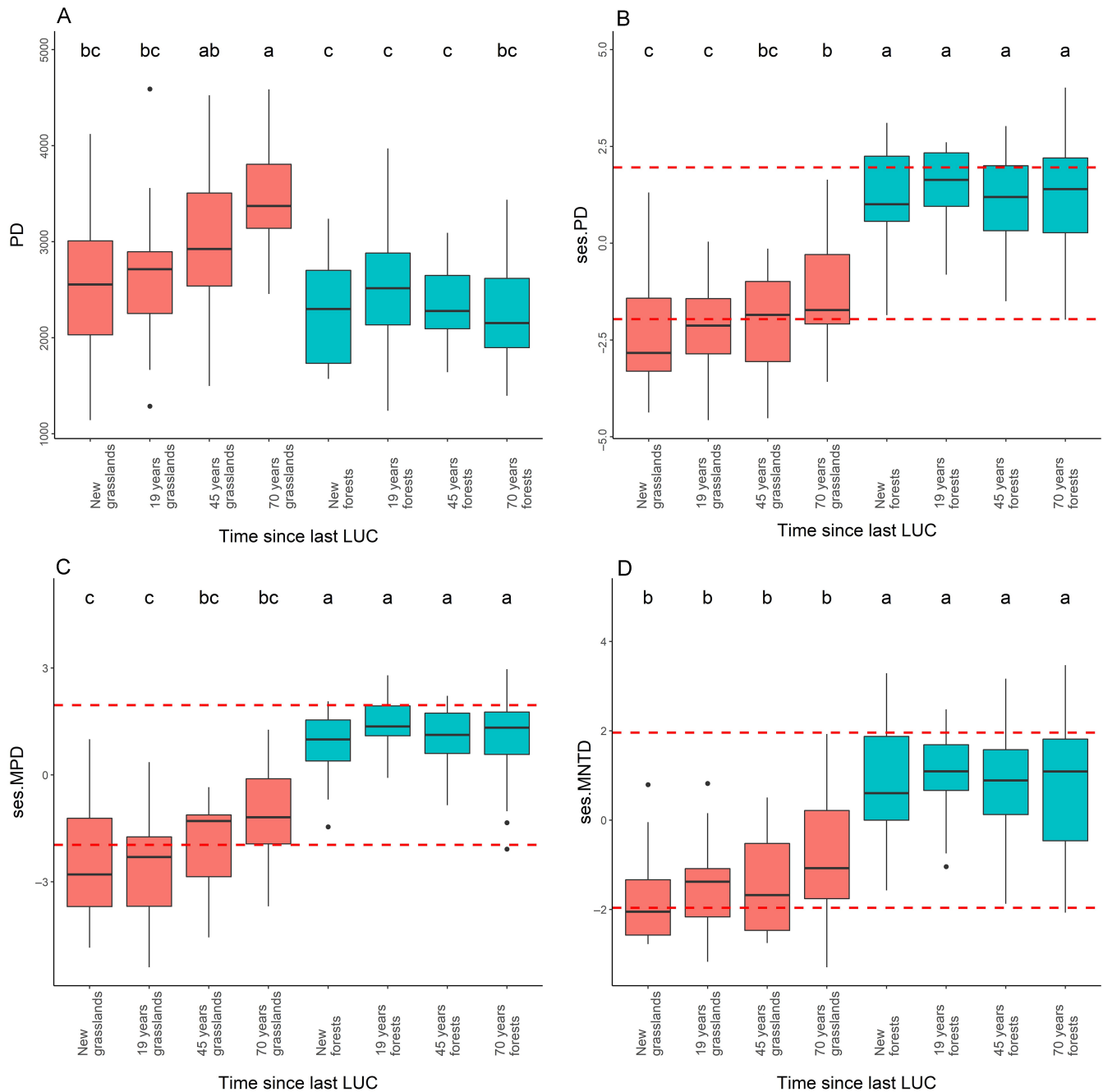


FIGURE 6 (A) Faith's phylogenetic diversity (PD), (B) standardized effect sizes of Faith's PD (ses.PD), (C) standardized effect sizes of mean phylogenetic distance (ses.MPD), and (D) standardized effect sizes of mean nearest taxon distance (ses.MNTD) between taxa. All metrics have been calculated based on angiosperm taxa recorded in the sampled plots. Values < -1.96 indicate significant phylogenetic clustering, whereas values > 1.96 indicate significant phylogenetic overdispersion (according to the "richness" null model). The threshold values are indicated by dashed red lines. The boxplots show medians, quartiles, 5–95 percentiles, and extreme values. Lowercase letters above boxplots represent ANOVA and post hoc Tukey test results. Red boxes represent grassland communities while blue boxes represent forest communities. LUC, land use change.

Effects of environmental variables and CSR strategies on PD patterns

Despite its key importance, community differentiation was not the only variable found to account for PD

patterns. R life strategy of plants was also found to explain a high percentage of PD and structure patterns (24.20%, 30.94%, and 17.86% relative influence regarding the ses.PD, ses.MPD, and ses.MNTD metrics, respectively). Particularly, phylogenetic structure metrics were

linearly correlated with R and C plant life strategies, with phylogenetic clustering occurring under higher R and lower C scores of plant communities, while phylogenetic randomness and overdispersion were observed under opposite patterns of R and C scores. Since R and C scores reflect the levels of disturbance and competition in plant communities, their simultaneous investigation along with PD metrics can be particularly informative. For example, the effects of disturbance in a community and the subsequent extinction of species vulnerable to disturbances have been suggested to result in reduced levels of competition in community assembly, and therefore nonrandom changes in PD by disproportionately affecting some lineages more than others (Mace et al., 2003). Such a potential role of PD patterns as proxies of community assembly mechanisms has been particularly challenged, since it is based on a number of assumptions that are not always adequately supported (Gerhold et al., 2015). Nevertheless, the herein inferred drivers of community assembly (differentiation of habitat, disturbance regime, and competition effects) are not assumed but rather supported by numerical data (vegetation community, R and C scores), therefore allowing safer inferences regarding the relations of PD patterns with the observed communities.

The three grassland communities that were found to be phylogenetically clustered, namely old fields with *H. bulbosum*, hay meadows with *A. rendlei*, and wet meadows with *C. cristatus*, are the communities that are submitted to more frequent but distinct anthropogenic disturbances due to different management regimes. Specifically, old fields with *H. bulbosum* are mainly submitted to infrequent mowing and more rarely plowing, hay meadows with *A. rendlei* are submitted to annual mowing and relatively intensive grazing by cattle, goats, and sheep, while wet meadows with *C. cristatus* are mostly grazed by goats and sheep. All the above communities may also be considered as pioneer as either they were developed soon after farmland abandonment or are subjected to intense and frequent disturbances not allowing continuation of succession. Disturbance has been previously identified as a main driver of PD of old field communities, with disturbed plant communities being phylogenetically clustered while undisturbed communities being phylogenetically random (Dinnage, 2009). Additionally, successional dynamics and grazing intensity have been found to affect PD (Larkin et al., 2015; Zhu et al., 2020). Zhu et al. (2020) found that the compositional changes in communities under intensive grazing were characterized by local extinctions of phylogenetically distinct species and establishment of phylogenetically similar colonizers, leading to phylogenetic clustering. Other types of disturbances, such as fire management and mowing,

have been also found to have similar effects on PD (Chollet et al., 2018; Pérez-Valera et al., 2018). PD and structure, although to a lower level, were statistically significantly correlated with the plant life strategy of stress tolerance as well. Particularly, positive correlation was observed, between phylogenetic metrics and stress tolerance, mostly for grassland communities. Lososová et al. (2021) attributed the clustered phylogenetical structure of some early successional vegetation types to a combined effect of stress and disturbance, which lead to a decreased number of plant lineages that can tolerate such conditions.

Several studies have revealed the low importance of abiotic variables on PD and structure of grassland and forest communities (Belinchón et al., 2019; Gerhold et al., 2013; Purschke et al., 2017). For example, Padullés Cubino et al. (2021) observed that environmental variables, including temperature and precipitation seasonality and soil pH and topographic factors, had low explanatory power for the phylogenetic structure of broadleaved deciduous forests. Similarly, in our study, the employed topographic, edaphic, and climatic factors were found to explain a relatively small percentage of total variation of phylogenetic structure of the studied communities (24.65%, 15.82%, and 26.04% additive percentage of all topographic, edaphic, and climatic factors together, for the ses.PD, ses.MPD, and ses.MNTD metrics, respectively). However, the insignificant relation of PD and structure with environmental variables may be because plant assemblages include evolutionary heritage from different geological time periods and its relation with the present-day environment may be hindered, unless it is examined on the basis of lineages from certain geological time periods (Bartish et al., 2016).

Effects of time since land use change on PD patterns

The great effect of disturbance on the diversity and structure of the studied vegetation plots is becoming more prevalent when phylogenetic metrics are investigated across the four classes of land use change per vegetation type. Particularly, higher percentages of not only new grasslands but also 19-year-old and 45-year-old grasslands were found to be phylogenetically clustered, while most of the >70-year-old grasslands were found to be phylogenetically random. This pattern of change during the >70-year-long succession from arable land to grasslands is in agreement with previous studies, which report a replacement of closely related species by more distinct species during the latest stages of the investigated chronosequences after disturbances and land abandonment (Dinnage, 2009; Purschke et al., 2013; Römermann

et al., 2009). In agreement with our findings, Purschke et al. (2013) also observed low levels of PD during the first 50 years after land abandonment, with a subsequent increase of PD in grasslands with more than 50 years of continuity. It should be noted, however, that the two grassland communities with the highest percentages of the class >70-year-old (*C. gryllus* and *P. fruticosa* communities) can be considered as more or less stable communities in which the succession is proceeding very slowly and their age is probably higher than 70 years. Thus, their different profile regarding PD and structure may be attributed, at least partly, to the abovementioned fact. Similarly, Belinchón et al. (2019) found different patterns concerning the relation of PD of grasslands with landscape characteristics according to their age, with new grasslands related mainly to present-day landscape configuration while old grasslands related to historical landscape configuration.

We observed similar trends between the metrics of PD and structure (ses.PD, ses.MPD, and ses.MNTD) along the succession gradient, with phylogenetic clustering decreasing from the grassland communities that were sampled shortly after their transition from arable land to abandoned fields toward the grasslands that have not been cultivated for >70 years. For forest communities, we did not observe any significant trend of differentiation of the PD and structure depending on the time since the last change in land use. Turley and Brudvig (2016), in a case study conducted in post-agricultural pine plantations compared to remnant longleaf pine savanna communities, observed lower levels of PD (ses.PD) in the post agricultural plant communities than in the remnant communities, but they did not observe any statistically significant differences regarding phylogenetic structure (ses.MPD). We consider that the contradiction of our results with the latter study can be attributed to the characteristics of the studied vegetation type. Specifically, communities dominated by pine species are usually open forest ecosystems that allow the establishment of light-demanding species along with species of forest ecosystems, justifying the similarity of the observed patterns with the ones we found for the grassland communities.

Low levels of phylogenetic clustering/overdispersion and potential causes

On the basis of theoretical assumptions, phylogenetic structure is expected to differ among communities under different levels of competition and environmental filtering (Kraft et al., 2007; Webb et al., 2002). Within the context of succession, environmental filtering is mainly represented by the effects of disturbance by selecting for

closely related species, while competition becomes more prevalent over time and selects for more distantly related species in late successional stages (Connell & Slatyer, 1977). Such a transition, from early successional stages soon after land abandonment submitted to low levels of competition toward later successional stages dominated by more competitive taxa, accompanied by changes in their PD and structure, is also observed in our study. Specifically, high levels of competition are observed in all forest communities, with the two more mesic communities of *Q. frainetto* forests and *Q. cerris*-*Q. frainetto* mixed forests, as well as the riparian forests having higher levels of competition. According to theory, such a high level of competition would lead to phylogenetic overdispersion, but in our case, although all forest communities include some phylogenetically overdispersed plots, their general observed structure was randomness. Therefore, although a gradient of competition level was observed not only among all communities but also within grassland and forest types, competition effects were not found to lead to phylogenetic overdispersion, similar to the findings of other studies (Bennett et al., 2013; Goberna et al., 2014; Li et al., 2015). This could be the result of the counteractive effects of stress due to low resource availability per individual in late successional environments (Grime, 1987).

Phylogenetic randomness has been previously observed for oak forests and oriental hornbeam forests in Greece (Mastrogianni et al., 2019), while Padullés Cubino et al. (2021) also demonstrated that most communities of broadleaved deciduous forests are characterized by phylogenetic randomness in our general study area. In fact, among all types of broadleaved deciduous forests, and across Europe, only boreal and nemoral mountain *Betula* forests were found to be phylogenetically clustered, temperate, and boreal hardwood riparian forests and ravine forests were phylogenetically overdispersed, while the remaining broadleaved deciduous forest types were phylogenetically random (Padullés Cubino et al., 2021). In agreement with these findings, we also observed phylogenetic overdispersion for riparian forests, although these results should be interpreted with caution due to the low number of available plots for this community.

A high percentage of vegetation plots was found to have random phylogenetic structure. The observed levels of clustering or overdispersion depend on the total species pool of each study. Particularly, investigation of phylogenetic structure within a small species pool can lead to observation of random patterns, while usage of a very large species pool can lead to the identification of clustering (Swenson et al., 2006). In order to understand the potential effects of this factor, we conducted additional analyses of all phylogenetic metrics for grasslands and

forests separately (not presented here) and weak patterns of clustered or overdispersed structure were observed (20.8%, 6.4%, and 13.2% of plots were found clustered or overdispersed for the ses.PD, ses.MPD, and ses.MNTD metric, respectively). After calculating PD metrics for all sampled vegetation plots together, a significantly greater number of plots was identified to have a nonrandom pattern of PD and structure (42%, 30.4%, and 25.2% of plots were found clustered or overdispersed for the ses.PD, ses.MPD, and ses.MNTD metric, respectively). Similar to these findings, several studies that investigate the effects of succession, land use changes, or disturbance on the phylogenetic structure of plant communities have found no statistically significant patterns of community structure when investigating only one type of habitat (Belinchón et al., 2019; Egorov et al., 2014), contrary to the results of studies that included various types of habitats, which were able to identify statistically significant nonrandom diversity and structure patterns for some of the studied plant communities (Chai et al., 2016; Kusuma et al., 2018; Lososová et al., 2021; Morel et al., 2020; Villalobos & Vamosi, 2016). Thus, it is becoming apparent that the interpretation of results derived from such metrics should be made with caution after taking into account the nature of the employed dataset. In our case, the finally observed random patterns are probably not the result of a narrow species pool including only close relative taxa, since inclusion of all vegetation units occurring in the study area (i.e., both grassland and forest communities) allowed the identification of more statistically significant patterns. Nevertheless, enlarging our study area and thus including additional environmental and thus vegetation diversity might lead to a further increase in the percentage of phylogenetically nonrandom vegetation plots.

CONCLUSIONS

PD and structure varied significantly between grassland and forest communities, with forests having higher levels of diversity, which was attributed to their greater habitat age at a geological time scale compared with grasslands. Level of disturbance was found to be the main driver of phylogenetic clustering in grassland vegetation plots by disproportionately affecting specific plant lineages through filtering effects. Competition and environmental variables were to a lesser extent good predictors of phylogenetic patterns. Overall, PD and structure were found to be lower and clustered for grassland communities shortly after the cessation of agricultural activities, but a similar pattern was not detected for forests, whose diversity patterns were not differentiated in relation to time since land abandonment.

AUTHOR CONTRIBUTIONS

Ioannis Tsiripidis coordinated the study. Anna Mastrogianni conducted data analyses and prepared the first draft of the manuscript. All authors contributed to the conceptualization of the study, the field survey, as well as the final revision and editing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Mastrogianni et al., 2024) are available from Figshare: <https://doi.org/10.6084/m9.figshare.26335102>.

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REFERENCES

- Arroyo-Rodríguez, V., J. Cavender-Bares, F. Escobar, F. P. L. Melo, M. Tabarelli, and B. A. Santos. 2012. “Maintenance of Tree Phylogenetic Diversity in a Highly Fragmented Rain Forest.” *Journal of Ecology* 100: 702–711.
- Bartish, I. V., W. A. Ozinga, M. I. Bartish, G. W. W. Wamelink, S. M. Hennekens, and A. Prinzing. 2016. “Different Habitats within a Region Contain Evolutionary Heritage from Different Epochs Depending on the Abiotic Environment.” *Global Ecology and Biogeography* 25: 274–285.
- Behroozian, M., H. Ejtehadi, F. Memariani, S. Pierce, and M. Mesdaghi. 2020. “Are Endemic Species Necessarily Ecological Specialists? Functional Variability and Niche Differentiation of Two Threatened *Dianthus* Species in the Montane Steppes of Northeastern Iran.” *Scientific Reports* 10: 11774.
- Belinchón, R., L. Hemrová, and Z. Münzbergová. 2019. “Abiotic, Present-Day and Historical Effects on Species, Functional and Phylogenetic Diversity in Dry Grasslands of Different Age.” *PLoS One* 14: e0223826.
- Bennett, J. A., E. G. Lamb, J. C. Hall, W. M. Cardinal-McTeague, and J. F. Cahill, Jr. 2013. “Increased Competition Does Not Lead to Increased Phylogenetic Overdispersion in a Native Grassland.” *Ecology Letters* 16: 1168–76.
- Bernhardt-Römermann, M., A. Gray, A. J. Vanbergen, L. Bergès, A. Bohner, R. W. Brooker, L. De Bruyn, et al. 2011. “Functional Traits and Local Environment Predict Vegetation Responses to Disturbance: A Pan-European Multi-Site Experiment.” *Journal of Ecology* 99: 777–787.
- Braun-Blanquet, J. 1964. *Pflanzensoziologie*, 3rd ed. Berlin and New York: Springer Verlag.

- Cadotte, M. W., T. Jonathan Davies, J. Regetz, S. W. Kembel, E. Cleland, and T. H. Oakley. 2010. "Phylogenetic Diversity Metrics for Ecological Communities: Integrating Species Richness, Abundance and Evolutionary History." *Ecology Letters* 13: 96–105.
- Cadotte, M. W., and C. M. Tucker. 2017. "Should Environmental Filtering be Abandoned?" *Trends in Ecology & Evolution* 32: 429–437.
- Cardillo, M. 2023. "Phylogenetic Diversity in Conservation: A Brief History, Critical Overview, and Challenges to Progress." *Cambridge Prisms: Extinction* 1: e11.
- Carlucci, M. B., G. D. S. Seger, D. Sheil, I. L. Amaral, G. B. Chuyong, L. V. Ferreira, U. Galatti, et al. 2017. "Phylogenetic Composition and Structure of Tree Communities Shed Light on Historical Processes Influencing Tropical Rainforest Diversity." *Ecography* 40: 521–530.
- Chai, Y., M. Yue, X. Liu, Y. Guo, M. Wang, J. Xu, C. Zhang, Y. Chen, L. Zhang, and R. Zhang. 2016. "Patterns of Taxonomic, Phylogenetic Diversity during a Long-Term Succession of Forest on the Loess Plateau, China: Insights into Assembly Process." *Scientific Reports* 6: 1–10.
- Chollet, S., C. Brabant, S. Tessier, and V. Jung. 2018. "From Urban Lawns to Urban Meadows: Reduction of Mowing Frequency Increases Plant Taxonomic, Functional and Phylogenetic Diversity." *Landscape and Urban Planning* 180: 121–24.
- Chytrý, M., J. Danihelka, Z. Kaplan, J. Wild, D. Holubová, P. Novotný, M. Řezníčková, et al. 2021. "Pladias Database of the Czech Flora and Vegetation." *Preslia* 93: 1–87.
- Connell, J. H., and R. O. Slatyer. 1977. "Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization." *The American Naturalist* 111: 1119–44.
- Davies, T. J. 2021. "Ecophylogenetics Redux." *Ecology Letters* 24: 1073–88.
- Deák, B., Z. Rádai, K. Lukács, A. Kelemen, R. Kiss, Z. Bátor, P. J. Kiss, and O. Valkó. 2020. "Fragmented Dry Grasslands Preserve Unique Components of Plant Species and Phylogenetic Diversity in Agricultural Landscapes." *Biodiversity and Conservation* 29: 4091–4110.
- Debastiani, V. J., and L. S. Duarte. 2014. "PCPS – An R-Package for Exploring Phylogenetic Eigenvectors across Metacommunities." *Frontiers of Biogeography* 6:3.
- Dengler, J., F. Jansen, O. Chusova, E. Hüllbusch, M. P. Nobis, K. V. Meerbeek, I. Axmanová, et al. 2023. "Ecological Indicator Values for Europe (EIVE) 1.0." *Vegetation Classification and Survey* 4: 7–29.
- Dias, R. A., V. A. G. Bastazini, B. C. Knopp, F. C. Bonow, M. S. S. Gonçalves, and A. T. Gianuca. 2020. "Species Richness and Patterns of Overdispersion, Clustering and Randomness Shape Phylogenetic and Functional Diversity–Area Relationships in Habitat Islands." *Journal of Biogeography* 47: 1638–48.
- Dinnage, R. 2009. "Disturbance Alters the Phylogenetic Composition and Structure of Plant Communities in an Old Field System." *PLoS One* 4: e7071.
- Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. "Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss." *Science* 344: 296–99.
- Duarte, L. S. 2011. "Phylogenetic Habitat Filtering Influences Forest Nucleation in Grasslands." *Oikos* 120: 208–215.
- Duarte, L. S., P. V. Prieto, and V. D. Pillar. 2012. "Assessing Spatial and Environmental Drivers of Phylogenetic Structure in Brazilian Araucaria Forests." *Ecography* 35: 952–960.
- Egorov, E., D. Prati, W. Durka, S. Michalski, M. Fischer, B. Schmitt, S. Blaser, and M. Brändle. 2014. "Does Land-Use Intensification Decrease Plant Phylogenetic Diversity in Local Grasslands?" *PLoS One* 9: e103252.
- Elith, J., J. R. Leathwick, and T. Hastie. 2008. "A Working Guide to Boosted Regression Trees." *Journal of Animal Ecology* 77: 802–813.
- Faith, D. P. 1992. "Conservation Evaluation and Phylogenetic Diversity." *Biological Conservation* 61: 1–10.
- Faith, D. P. 1994. "Phylogenetic Pattern and the Quantification of Organismal Biodiversity." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 345: 45–58.
- Forest, F., R. Grenyer, M. Rouget, T. J. Davies, R. M. Cowling, D. P. Faith, A. Balmford, et al. 2007. "Preserving the Evolutionary Potential of Floras in Biodiversity Hotspots." *Nature* 445: 757–760.
- Gerhold, P., J. F. Cahill, M. Winter, I. V. Bartish, and A. Prinzing. 2015. "Phylogenetic Patterns Are Not Proxies of Community Assembly Mechanisms (They Are Far Better)." *Functional Ecology* 29: 600–614.
- Gerhold, P., M. B. Carlucci, Ş. Procheş, and A. Prinzing. 2018. "The Deep Past Controls the Phylogenetic Structure of Present, Local Communities." *Annual Review of Ecology, Evolution, and Systematics* 49: 477–497.
- Gerhold, P., M. Pärtel, J. Liira, K. Zobel, and A. Prinzing. 2008. "Phylogenetic Structure of Local Communities Predicts the Size of the Regional Species Pool." *Journal of Ecology* 96: 709–712.
- Gerhold, P., J. N. Price, K. Püssa, R. Kalamees, K. Aher, A. Kaasik, and M. Pärtel. 2013. "Functional and Phylogenetic Community Assembly Linked to Changes in Species Diversity in a Long-Term Resource Manipulation Experiment." *Journal of Vegetation Science* 24: 843–852.
- Goberna, M., J. A. Navarro-Cano, A. Valiente-Banuet, C. García, and M. Verdú. 2014. "Abiotic Stress Tolerance and Competition-Related Traits Underlie Phylogenetic Clustering in Soil Bacterial Communities." *Ecology Letters* 17: 1191–1201.
- Gower, J. C. 1966. "Some Distance Properties of Latent Root and Vector Methods Used in Multivariate Analysis." *Biometrika* 53: 325–338.
- Grime, J. 1974. "Vegetation Classification by Reference to Strategies." *Nature* 250: 26–31.
- Grime, J. 1977. "Evidence for the Existence of Three Primary Strategies in Plants and its Relevance to Ecological and Evolutionary Theory." *The American Naturalist* 111: 1169–94.
- Grime, J. 1987. "Dominant and Subordinate Components of Plant Communities: Implications for Succession, Stability and Diversity." In *26th Symposium of the British Ecological Society*, edited by A. Gray, M. Crawley, and P. Edwards. Oxford: Blackwell Scientific.
- Grime, J. 2001. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd ed. New York: John Wiley & Sons.
- Hastie, T., R. Tibshirani, and J. Friedman. 2009. *The Elements of Statistical Learning. Data Mining, Inference, and Prediction*. New York: Springer Series in Statistics, 2nd ed.

- Helmus, M. R., T. J. Bland, C. K. Williams, and A. R. Ives. 2007. "Phylogenetic Measures of Biodiversity." *The American Naturalist* 169: E68–E83.
- Helmus, M. R., W. B. Keller, M. J. Paterson, N. D. Yan, C. H. Cannon, and J. A. Rusak. 2010. "Communities Contain Closely Related Species during Ecosystem Disturbance." *Ecology Letters* 13: 162–174.
- Hodgson, J. G., P. J. Wilson, R. Hunt, J. P. Grime, and K. Thompson. 1999. "Allocating C-S-R Plant Functional Types: A Soft Approach to a Hard Problem." *Oikos* 85: 282–294.
- Hsieh, T. C., K. H. Ma, and A. Chao. 2016. "iNEXT: An R Package for Rarefaction and Extrapolation of Species Diversity (Hill Numbers)." *Methods in Ecology and Evolution* 7: 1451–56.
- Jin, Y., and H. Qian. 2019. "V.PhyloMaker: An R Package that Can Generate Very Large Phylogenies for Vascular Plants." *Ecography* 42: 1353–59.
- Karger, D. N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-Auza, N. E. Zimmermann, H. P. Linder, and M. Kessler. 2017. "Climatologies at High Resolution for the Earth's Land Surface Areas." *Scientific Data* 4: 170122.
- Kiziridis, D. A., A. Mastrogianni, M. Pleniou, E. Karadimou, S. Tsiftsis, F. Xystrakis, and I. Tsiripidis. 2022. "Acceleration and Relocation of Abandonment in a Mediterranean Mountainous Landscape: Drivers, Consequences, and Management Implications." *Land* 11: 406.
- Kraft, N. J. B., W. K. Cornwell, C. O. Webb, and D. D. Ackerly. 2007. "Trait Evolution, Community Assembly, and the Phylogenetic Structure of Ecological Communities." *The American Naturalist* 170: 271–283.
- Kubota, Y., B. Kusumoto, T. Shiono, and W. Ulrich. 2018. "Environmental Filters Shaping Angiosperm Tree Assembly along Climatic and Geographic Gradients." *Journal of Vegetation Science* 29: 607–618.
- Kusuma, Y. W. C., K. Rembold, S. S. Tjitrosoedirdjo, and H. Kreft. 2018. "Tropical Rainforest Conversion and Land Use Intensification Reduce Understorey Plant Phylogenetic Diversity." *Journal of Applied Ecology* 55: 2216–26.
- Larkin, D. J., A. L. Hipp, J. Kattge, W. Prescott, R. K. Tonietto, S. K. Jacobi, and M. L. Bowles. 2015. "Phylogenetic Measures of Plant Communities Show Long-Term Change and Impacts of Fire Management in Tallgrass Prairie Remnants." *Journal of Applied Ecology* 52: 1638–48.
- Lavorel, S., K. Grigulis, S. McIntyre, N. S. G. Williams, D. Garden, J. Dorrrough, S. Berman, F. Quéfier, A. Thébault, and A. Bonis. 2008. "Assessing Functional Diversity in the Field – Methodology Matters!" *Functional Ecology* 22: 134–147.
- Legendre, P., and E. D. Gallagher. 2001. "Ecologically Meaningful Transformations for Ordination of Species Data." *Oecologia* 129: 271–280.
- Legendre, P., and L. Legendre. 1998. *Numerical Ecology*, 2nd ed., 870. Amsterdam: Elsevier.
- Letcher, S. G. 2010. "Phylogenetic Structure of Angiosperm Communities during Tropical Forest Succession." *Proceedings of the Royal Society B: Biological Sciences* 277: 97–104.
- Levers, C., M. Schneider, A. V. Prishchepov, S. Estel, and T. Kuemmerle. 2018. "Spatial Variation in Determinants of Agricultural Land Abandonment in Europe." *Science of the Total Environment* 644: 95–111.
- Li, S., M. W. Cadotte, S. J. Meiners, Z. Hua, L. Jiang, and W. Shu. 2015. "Species Colonisation, Not Competitive Exclusion, Drives Community Overdispersion over Long-Term Succession." *Ecology Letters* 18: 964–973.
- Li, Y., and B. Shipley. 2017. "An Experimental Test of CSR Theory Using a Globally Calibrated Ordination Method." *PLoS One* 12: e0175404.
- Liarikas, K., P. Maragkou, and T. Papayiannis. 2012. *Greece Then and Now: Temporal Mapping of Land Use, 1987–2007*. Athens: WWF Hellas.
- Lososová, Z., J. Divíšek, M. Chytrý, L. Götzenberger, J. Těšitel, and L. Mucina. 2021. "Macroevolutionary Patterns in European Vegetation." *Journal of Vegetation Science* 32: e12942.
- Lososová, Z., P. Šmarda, M. Chytrý, O. Purschke, P. Pyšek, J. Sádlo, L. Tichý, and M. Winter. 2015. "Phylogenetic Structure of Plant Species Pools Reflects Habitat Age on the Geological Time Scale." *Journal of Vegetation Science* 26: 1080–89.
- MacDonald, D., J. R. Crabtree, G. Wiesinger, T. Dax, N. Stamou, P. Fleury, J. Gutierrez Lazpita, and A. Gibon. 2000. "Agricultural Abandonment in Mountain Areas of Europe: Environmental Consequences and Policy Response." *Journal of Environmental Management* 59: 47–69.
- Mace, G. M., J. L. Gittleman, and A. Purvis. 2003. "Preserving the Tree of Life." *Science* 300: 1707–9.
- Mächler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2012. "Cluster: Cluster Analysis Basics and Extensions." Version 2.0.4. <https://svn.r-project.org/R-packages/trunk/cluster/>
- Massante, J. C., L. Götzenberger, K. Takkis, T. Hallikma, A. Kaasik, L. Laanisto, M. J. Hutchings, and P. Gerhold. 2019. "Contrasting Latitudinal Patterns in Phylogenetic Diversity between Woody and Herbaceous Communities." *Scientific Reports* 9: 6443.
- Mastrogianni, A., A. S. Kallimanis, M. Chytrý, and I. Tsiripidis. 2019. "Phylogenetic Diversity Patterns in Forests of a Putative Refugial Area in Greece: A Community Level Analysis." *Forest Ecology and Management* 446: 226–237.
- Mastrogianni, A., D. A. Kiziridis, E. Karadimou, M. Pleniou, F. Xystrakis, S. Tsiftsis, and I. Tsiripidis. 2023. "Community-Level Differentiation of Grime's CSR Strategies along a Post-Abandonment Secondary Successional Gradient." *Flora* 308: 152399.
- Mastrogianni, A., I. Tsiripidis, D. Kiziridis, M. Pleniou, F. Xystrakis, and S. Tsiftsis. 2024. "Imprints of Land Use History and Disturbance Regime in Phylogenetic Diversity of Mediterranean Plant Communities." Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.26335102.v1>.
- Mazel, F., T. J. Davies, L. Gallien, J. Renaud, M. Groussin, T. Münkemüller, and W. Thuiller. 2016. "Influence of Tree Shape and Evolutionary Time-Scale on Phylogenetic Diversity Metrics." *Ecography* 39: 913–920.
- McCune, B., and J. Grace. 2002. *Analysis of Ecological Communities*. Oregon: MjM Software Design.
- Miller, E. T., D. R. Farine, and C. H. Trisos. 2017. "Phylogenetic Community Structure Metrics and Null Models: A Review with New Methods and Software." *Ecography* 40: 461–477.
- Morel, L., L. Barbe, V. Jung, B. Clément, A. Schnitzler, and F. Ysnel. 2020. "Passive Rewilding May (Also) Restore Phylogenetically Rich and Functionally Resilient Forest Plant Communities." *Ecological Applications* 30: e02007.

- Oppermann, R., G. Beaufoy, and G. Jones. 2012. *High Nature Value Farming in Europe: 35 European Countries – Experiences and Perspectives*. Ubstadt-Weiher: Verlag Regionalkultur.
- Padullés Cubino, J., Z. Lososová, G. Bonari, E. Agrillo, F. Attorre, E. Bergmeier, I. Biurrun, et al. 2021. “Phylogenetic Structure of European Forest Vegetation.” *Journal of Biogeography* 48: 903–916.
- Papanastasis, V. 2007. “Land Abandonment and Old Field Dynamics in Greece.” In *Old Fields: Dynamics and Restoration of Abandoned Farmland*, edited by V. A. Cramer and R. J. Hobbs, 225–246. Washington: Island Press
- Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, et al. 2013. “New Handbook for Standardised Measurement of Plant Functional Traits Worldwide.” *Australian Journal of Botany* 61: 167–234.
- Pérez-Valera, E., M. Verdú, J. A. Navarro-Cano, and M. Goberna. 2018. “Resilience to Fire of Phylogenetic Diversity across Biological Domains.” *Molecular Ecology* 27: 2896–2908.
- Petermann, J. S., and O. Y. Buzhdygan. 2021. “Grassland Biodiversity.” *Current Biology* 31: R1195–R1201.
- Pierce, S., D. Negreiros, B. E. L. Cerabolini, J. Kattge, S. Díaz, M. Kleyer, B. Shipley, et al. 2017. “A Global Method for Calculating Plant CSR Ecological Strategies Applied across Biomes World-Wide.” *Functional Ecology* 31: 444–457.
- Podani, J. 2006. “Braun-Blanquet’s Legacy and Data Analysis in Vegetation Science.” *Journal of Vegetation Science* 17: 113–17.
- Poggio, L., L. M. de Sousa, N. H. Batjes, G. B. M. Heuvelink, B. Kempen, E. Ribeiro, and D. Rossiter. 2021. “SoilGrids 2.0: Producing Soil Information for the Globe with Quantified Spatial Uncertainty.” *The Soil* 7: 217–240.
- Prach, K., K. Řehounková, K. Lencová, A. Jírová, P. Konvalinková, O. Mudrák, V. Študent, et al. 2014. “Vegetation Succession in Restoration of Disturbed Sites in Central Europe: The Direction of Succession and Species Richness across 19 Seres.” *Applied Vegetation Science* 17: 193–200.
- Purschke, O., S. G. Michalski, H. Bruelheide, and W. Durka. 2017. “Phylogenetic Turnover during Subtropical Forest Succession across Environmental and Phylogenetic Scales.” *Ecology and Evolution* 7: 11079–91.
- Purschke, O., B. C. Schmid, M. T. Sykes, P. Poschlod, S. G. Michalski, W. Durka, I. Kühn, M. Winter, and H. C. Prentice. 2013. “Contrasting Changes in Taxonomic, Phylogenetic and Functional Diversity during a Long-Term Succession: Insights into Assembly Processes.” *Journal of Ecology* 101: 857–866.
- Qian, H., and Y. Jin. 2021. “Are Phylogenies Resolved at the Genus Level Appropriate for Studies on Phylogenetic Structure of Species Assemblages?” *Plant Diversity* 43: 255–263.
- Queiroz, C., R. Beilin, C. Folke, and R. Lindborg. 2014. “Farmland Abandonment: Threat or Opportunity for Biodiversity Conservation? A Global Review.” *Frontiers in Ecology and the Environment* 12: 288–296.
- R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Ricklefs, R. E. 2004. “A Comprehensive Framework for Global Patterns in Biodiversity.” *Ecology Letters* 7: 1–15.
- Römermann, C., M. Bernhardt-Römermann, M. Kleyer, and P. Poschlod. 2009. “Substitutes for Grazing in Semi-Natural Grasslands – Do Mowing or Mulching Represent Valuable Alternatives to Maintain Vegetation Structure?” *Journal of Vegetation Science* 20: 1086–98.
- Rosenfield, M. F., S. C. Müller, and G. E. Overbeck. 2019. “Short Gradient, but Distinct Plant Strategies: The CSR Scheme Applied to Subtropical Forests.” *Journal of Vegetation Science* 30: 984–993.
- Sluiter, R., and S. M. de Jong. 2007. “Spatial Patterns of Mediterranean Land Abandonment and Related Land Cover Transitions.” *Landscape Ecology* 22: 559–576.
- Smith, S. A., and J. W. Brown. 2018. “Constructing a Broadly Inclusive Seed Plant Phylogeny.” *American Journal of Botany* 105: 302–314.
- Soliveres, S., R. Torices, and F. T. Maestre. 2012. “Environmental Conditions and Biotic Interactions Acting Together Promote Phylogenetic Randomness in Semi-Arid Plant Communities: New Methods Help to Avoid Misleading Conclusions.” *Journal of Vegetation Science* 23: 822–836.
- Strömberg, C. A. E. 2011. “Evolution of Grasses and Grassland Ecosystems.” *Annual Review of Earth and Planetary Sciences* 39: 517–544.
- Subedi, Y. R., P. Kristiansen, and O. Cacho. 2022. “Drivers and Consequences of Agricultural Land Abandonment and Its Reutilisation Pathways: A Systematic Review.” *Environment and Development* 42: 100681.
- Swenson, N. G., B. J. Enquist, J. Pither, J. Thompson, and J. K. Zimmerman. 2006. “The Problem and Promise of Scale Dependency in Community Phylogenetics.” *Ecology* 87(10): 2418–24.
- Tichý, L., and M. Chytrý. 2006. “Statistical Determination of Diagnostic Species for Site Groups of Unequal Size.” *Journal of Vegetation Science* 17: 809–818.
- Tucker, C. M., and M. W. Cadotte. 2013. “Unifying Measures of Biodiversity: Understanding when Richness and Phylogenetic Diversity Should be Congruent.” *Diversity and Distributions* 19: 845–854.
- Tucker, C. M., M. W. Cadotte, S. B. Carvalho, T. J. Davies, S. Ferrier, S. A. Fritz, R. Grenyer, et al. 2017. “A Guide to Phylogenetic Metrics for Conservation, Community Ecology and Macroecology.” *Biological Reviews* 92: 698–715.
- Turley, N. E., and L. A. Brudvig. 2016. “Agricultural Land-Use History Causes Persistent Loss of Plant Phylogenetic Diversity.” *Ecology* 97: 2240–47.
- Uchida, K., M. K. Hiraiwa, and M. W. Cadotte. 2019. “Non-random Loss of Phylogenetically Distinct Rare Species Degrades Phylogenetic Diversity in Semi-Natural Grasslands.” *Journal of Applied Ecology* 56: 1419–28.
- Villalobos, S., and J. C. Vamosi. 2016. “Increasing Land Use Drives Changes in Plant Phylogenetic Diversity and Prevalence of Specialists.” *PeerJ* 4: e1740.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. “Phylogenies and Community Ecology.” *Annual Review of Ecology and Systematics* 33: 475–505.
- Weissteiner, C. J., M. Boschetti, K. Böttcher, P. Carrara, G. Bordogna, and P. A. Brivio. 2011. “Spatial Explicit Assessment of Rural Land Abandonment in the Mediterranean Area.” *Global and Planetary Change* 79: 20–36.
- Westhoff, V., and E. Van Der Maarel. 1978. “The Braun-Blanquet Approach.” In *Classification of Plant Communities*, edited by R. H. Whittaker, 287–399. Dordrecht: Springer.

- Wilmanns, O. 1989. *Ökologische Pflanzensoziologie*, 4th ed. Heidelberg: Aufl. Quelle & Meyer.
- Zanzottera, M., M. Dalle Fratte, M. Caccianiga, S. Pierce, and B. E. L. Cerabolini. 2020. "Community-Level Variation in Plant Functional Traits and Ecological Strategies Shapes Habitat Structure along Succession Gradients in Alpine Environment." *Community Ecology* 21: 55–65.
- Zhang, J., S. J. Mayor, and F. He. 2014. "Does Disturbance Regime Change Community Assembly of Angiosperm Plant Communities in the Boreal Forest?" *Journal of Plant Ecology* 7: 188–201.
- Zhu, J., Y. Zhang, W. Wang, X. Yang, N. Chen, R. Shen, L. Wang, and L. Jiang. 2020. "Species Turnover Drives Grassland Community to Phylogenetic Clustering over Long-Term Grazing Disturbance." *Journal of Plant Ecology* 13: 157–164.
- Zomeni, M., J. Tzanopoulos, and J. D. Pantis. 2008. "Historical Analysis of Landscape Change Using Remote Sensing Techniques: An Explanatory Tool for Agricultural

Transformation in Greek Rural Areas." *Landscape and Urban Planning* 86: 38–46.

SUPPORTING INFORMATION

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

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