Community-level differentiation of Grime's CSR strategies along a post-abandonment secondary successional gradient[☆]

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ABSTRACT

Understanding the ecological processes and the mechanisms of community assembly during secondary succession of vegetation has been a central topic of ecological research. In the last decades, it has also been rendered as a necessity for wildlife management due to the ongoing vegetation succession caused by land abandonment in many parts of the world. Here, we investigated the taxonomic and life strategies diversity patterns among vegetation communities representing a large part of a natural succession gradient, in a (sub-) mountainous area of northwestern Greece (northern Pindus). Sampling of grassland and forest vegetation plots was conducted across an area submitted to high levels of land abandonment during the last 70 years, accompanied with sampling of new functional trait data. The Grime's CSR model of plant strategies was employed to investigate functional diversity of communities, while climatic, edaphic and topographic factors were employed to identify potential drivers of alternative life strategies diversity. Additionally, alpha and beta taxonomic and life strategies diversity of communities were calculated. Variation partitioning analyses attributed functional and taxonomic differentiation of communities mainly to the legacy of land use cover. Overall, grasslands and forests were functionally differentiated, with forest communities having higher levels of the competitive strategy, and grasslands having higher levels of the ruderal strategy. Nevertheless, parallel trends of occurrence of plant life strategies were found for both grasslands and forests. Community level competitive and stress-tolerating plant life strategies were found to be strongly and negatively correlated with soil organic content, soil nitrogen, soil pH and slope, while ruderalism was largely related to the disturbance regime of each community. The derived information of functional strategies diversity can provide valuable data that can guide management actions and contribute to the optimization of systematic conservation planning in such high nature value and threatened ecosystems.

1. Introduction

Habitat and vegetation composition have been significantly influenced by land use changes over the last decades in most European regions (Poschlod et al., 2005; Stoate et al., 2009). Land abandonment has been particularly prominent in Europe throughout the 20th century, especially in mountainous regions, inherently corresponding to patterns of decrease and aging of rural populations (MacDonald et al., 2000; Sitzia et al., 2010). The abandonment of agricultural land refers to the process of ceasing of agricultural activities on cropland and grasslands,

followed by subsequent passive recovery of natural vegetation through secondary succession (Levers et al., 2018; MacDonald et al., 2000). Specifically, during secondary succession, plant species from surrounding habitats gradually disperse and establish in the abandoned arable land (Csecserits et al., 2011). As a result, regional biodiversity patterns are drastically affected, due to the alteration of species distributions, species pools, as well as the composition and ecological functionality of communities, from a status existing for decades or centuries to a new dynamic status (Pérez-Hernández and Gavilán, 2021). For example, habitat alteration, landscape homogenization and cessation of

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traditional land-use disturbance regime may significantly affect the persistence of species restricted to habitats representing early succession stages of vegetation (e.g., grasslands, meadows, heathlands) (Gustavsson et al., 2007; Römermann et al., 2009; Vassilev et al., 2011). However, such processes may lead to a passive restoration of forest habitats, favoring forest species, and contributing to the mitigation of climate change (Bell et al., 2020; Pereira and Navarro, 2015).

Taxonomic diversity metrics, despite being able to inform us about species composition and turnover among the different stages of secondary succession, provide information which is difficult to compare among habitats or areas with different species pools (Duckworth et al., 2000; Woodward and Cramer, 1996). Additionally, they are considered as less capable of adequately reflecting the ecological processes driving succession (Díaz and Cabido, 2001). Therefore, functional-type analyses have been proposed as complementary to species-based approaches (Walker, 1992), which allow comparisons among different communities (Hunt et al., 2004), and provide complementary insights into the interpretation and understanding of ecological processes.

Functional diversity of species, as well as of communities, are known to be affected by land use intensification and abandonment, possibly towards opposite directions (Cramer et al., 2008; Mayfield et al., 2010), due to drastic alterations caused by changes in functional diversity drivers such as species dispersal, size and composition of species pools, as well as due to the spatial and temporal distribution and variation of resources (Damschen et al., 2008; Fukami, 2015). Within this context, functional trait syndromes, referring to consistent trade-offs among plant functional traits, have been identified and established as useful tools for exploring complex species responses at a global scale (Agrawal, 2020; Diaz et al., 2004). Examples of commonly used functional syndromes are leaf (as well as roots and stem) economic spectrums, referring to multivariate correlations that confine the global diversity of leaf traits (as well as root and stem traits respectively) (Freschet et al., 2010; Reich, 2014; Wright et al., 2004), seed size and seed number (Foster and Janson, 1985), as well as the Grime's Competitor, Stress-tolerator-Ruderal (CSR) model of plant strategies (Grime, 2001, 1974).

Grime's model assumes that functional responses of plants vary across different intensities of stress and disturbance at a local site and can be employed to identify the functional signature of species and communities along environmental or successional gradients (Li and Shipley, 2017; Zanzottera et al., 2020). According to the CSR model, stress (constraints on production) and disturbance (physical damage) act as restricting aspects of vegetation, downgrading competition for resource acquisition among neighboring species (Grime, 1974). The initial methodology developed by Hodgson et al. (1999) for the allocation of functional strategies to herbaceous vascular plants across the CSR triangle was based on seven morphological and phenological traits. Substitution of these traits with only three, easily measured, leaf traits allowed the extension of the applicability of the method to both woody and herbaceous vascular plants, and across different biomes (Pierce et al., 2017, 2013). Application of the CSR model at the community level, for the investigation of a community's functional signature (Hunt et al., 2004), has been shown to be able to correctly predict a community's response to stress and disturbance in several case studies and experiments (e.g., Bricca et al., 2021; Guerra et al., 2021; Li and Shipley, 2017; Zanzottera et al., 2020).

The recent development of the field of trait-based ecology, combined with the general trend of extensive land use cover change, have raised an excellent opportunity to investigate the patterns of vegetation succession, which in turn can provide useful information regarding community assembly and the relative importance of processes such as environmental filtering and limiting similarity (Douma et al., 2012; Dyderski et al., 2016; Laine et al., 2021; Navas et al., 2010; Raevel et al., 2012). Recent research conducted in such areas previously submitted to long-term management while currently affected by land abandonment, by using specific plant traits, has demonstrated significant differences between the assembly mechanisms during the different succession

stages (Loranger et al., 2016). However, as Loranger et al. (2016) noticed, the study of vegetation succession under changes in functional characteristics has been surprisingly rare. Although the Grime's life strategies reflect important trade-offs in the leaf economics spectrum and the leaf size spectrum (Ricotta et al., 2023), to the best of our knowledge, they have rarely been elaborated in the study of vegetation succession (Caccianiga et al., 2006; Chen et al., 2022; Prévosto et al., 2011; Silva et al., 2015), even after the enhancement of their determination by the recently developed method by Pierce et al. (2017). Furthermore, research on vegetation succession by applying functional diversity characteristics has been mostly conducted in either grassland or forest ecosystems and studies exploring functional diversity along the whole length of a successional gradient (i.e. from pioneer communities of herbs to forest communities) are missing from the bibliography.

Here, we present such a case study, investigating community assembly during passive revegetation after land abandonment across grassland and forest habitats in a mountainous region of northwestern Greece, with history of frequent transitions between the occurrence of extensive land management practices and land abandonment (Papanastasis, 2007). This transitional regime has created a dynamic equilibrium between arable lands, rangelands and forests, making abandoned fields an integral component of the Greek landscape (Papanastasis, 2007). In such a landscape, we aimed at investigating: i) the differentiation of plant life strategies among the main vegetation types (forests and grasslands/shrublands), and among the communities occurring in the study area; ii) the differentiation of plant life strategies among the different successional stages; and iii) the climatic, soil and topographic variables related to these differentiations.

2. Methodology

2.1. Study area and vegetation sampling

The present study was conducted in the northwestern sub-mountainous region of the Pindus Mountains in Greece (Fig. 1). The study area was selected as a typical example of a sub-mountainous Mediterranean area which was historically (i.e., before the 2nd World War) submitted to high levels of exploitation by means of traditional practices (e.g., small-scale farmlands, pastoralism), but during the last decades traditional land uses have been abandoned and extensive changes in land cover have been recorded (Kiziridis et al., 2022; Liarikas et al., 2012; Zomeni et al., 2008). A total of five circular study sites, with a diameter of 6 km each and a total cover of 141.4 km^2, were selected based on a preliminary investigation, which allowed the identification of the areas with extensive but also representative changes of land use between the years 1945 and 2015. The distinction of five study sites, instead of using one single region, allowed the investigation of spontaneous succession across a wider range of landscape characteristics such as geological substrate, altitude and microclimatic conditions, as well as across areas with different legacies of land use changes. Elevation ranged from 248 to 1203 m, while the general area is characterized by gentle slopes (0–10°), reaching a maximum of 55° According to Köppen–Geiger climatic classification, the area belongs to the Csa type (Peel et al., 2007). The geological substrate of the study area is constituted by 50 % limestone, 25.4 % deposits, 18.9 % silicate and 5.7 % flysch (Nakos, 1991), and it entirely belongs to the vegetation formation of thermophilous deciduous oaks (Bohn et al., 2004), which represents the so-called climax vegetation of the study area.

Vegetation sampling was conducted in the vegetative period of 2020. In each circular study site, 25 grassland or shrubland vegetation plots with an area of 50 m^2 (2.5 × 20 m) as well as 25 forest vegetation plots with an area of 200 m^2 (10 × 20 m) were sampled, leading to a final dataset of 250 vegetation plots (125 in grasslands/shrublands and 125 in forests). 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;
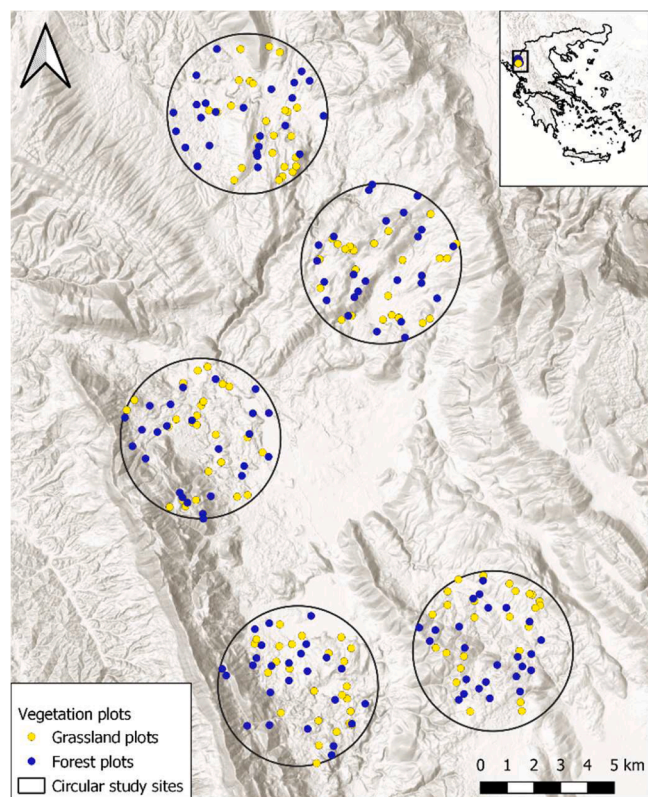
Fig. 1. Map of the study area, depicting the collection sites (circles) and the sampling plots (blue dots: forest plots, yellow dots: grassland plots) as well as their location in Greece (top right). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Wilmanns, 1989). Additionally, exact coordinates, altitude, slope, exposition as well as disturbance and grazing intensity were recorded for each vegetation plot.

2.2. Identification of vegetation succession patterns

Due to lack of historical vegetation records, succession was studied by employing the space-for-time substitution method (Pickett, 1989). For this reason, we conducted mapping of land cover in the general study area for four distinct periods, namely years 1945, 1970, 1996 and 2015. Five land type categories were identified during mapping, namely farmland (areas with evidence of agriculture and land management practices), grassland (cover of trees and shrubs in the 0–10 % range), open-scrub (cover of trees and shrubs 10–40 %), closed-scrub (cover of trees and shrubs 40–70 %) and forest (cover of trees and shrubs 70−100 %). For further details on mapping methodology and data sources, please see Kiziridis et al. (2022).

For each vegetation plot, we recorded the sequence of land type categories during the four periods of mapping, to explore any possible differentiation of the main vegetation succession stages due to effects of different time since vegetation establishment. The resulted data frame included four variables for each vegetation plot, representing the succession stage in which the locality of each plot was found in the four mapped periods. General succession stage was recorded as an ordinal variable expressed by the values 1 for the land cover of farmland, 2 for grassland, 3 for open scrub, 4 for closed scrub and 5 for forest. In this way we defined the expected time sequence that the vegetation succession stages would have if they were under an uninterrupted natural succession process. We used this data frame to perform a variation partitioning, as described in Section 2.5.

Furthermore, we intuitively ordered the distinguished plant communities occurring in the study area in a sequence that reflects their succession stage. We did this based on the floristic affinities-differences among the identified communities, their structure (i.e., species cover in the three vegetation layers, as well as height of shrub and tree layers), their ongoing disturbance regimes, as recorded during the two sampling years (2020–21), and their past disturbance regimes as inferred by the land cover category identified for each sampling plot of the communities, through mapping for the years 1945, 1970, 1996 and 2015. The rationale of such an ordering can be described as follows: a) communities dominated by grasses and forbs, being established mainly in the last one or two decades and being affected by frequent and intensive disturbances (i.e., mowing and grazing) were considered as early succession stages, hereafter mentioned as early grassland succession stage, b) communities dominated by grasses and forbs, but being encroached by woody species and affected by more extensive, rather than intensive disturbances were considered of more advanced succession stage than the former, hereafter mentioned as ongoing grassland succession stage c) communities dominated by grasses and forbs, submitted to more or less extensive grazing and with long-term stability of vegetation structure in their localities (even from 1945) were considered as stable (i.e., having a very slow succession process) in an advanced but stable succession stage, hereafter mentioned as advanced stable grassland succession stage d) communities having a closed (i.e. higher than 70 %) canopy of high shrubs and/or low trees, evident from the land cover mapping, which currently (i.e., during the sampling years) reflects the effects of past disturbances were considered as stable in a late succession stage, hereafter mentioned as advanced stable forest succession stage, and e) forest communities having a closed canopy of relatively high trees, and representing the potential vegetation type (zonal or riparian) of the area were consider in a late succession stage, hereafter mentioned as late forest succession stage.

2.3. Functional strategies (CSR scores) data

The methodology for classification of plant taxa in different CSR strategies has been developed and refined over several years (Grime, 1977; Hodgson et al., 1999; Pierce et al., 2017, 2013). "StrateFy", the most recent approach of CSR ordination (Pierce et al., 2017, 2013), has been proved to be easy to apply at the global scale, as well as able to correctly predict the expected responses of taxa to stress and disturbance (Li and Shipley, 2017). For the application of this method, three functional traits are required, namely leaf area, leaf dry matter content and specific leaf area (Pierce et al., 2017). A database of these functional traits per taxon occurring in the sampled vegetation plot was created by collecting new functional trait data from the study area. In total, 620 taxa were found to occur in the plots. From these, 153 taxa were occurring only in one or two plots, and were excluded from further analyses. For the collection of functional trait data of the remaining 468 taxa, we revisited vegetation plots during the vegetative period of 2021. We found and collected 5 ± 2 well-developed individuals for 408 taxa (87.2 %), and their leaf area (LA; mm^2), leaf dry matter content (LDMC: leaf dry weight/water-saturated leaf weight; mg/g) and specific leaf area (SLA: leaf area/leaf dry weight; mm^2 /mg) were measured, following standard protocols (Pérez-Harguindeguy et al., 2013). Subsequently, we allocated CSR scores for each species, by using the centroid values of the CSR strategies calculated for all sampled individuals per taxon (Mastrogianni et al., 2023), by the application of the "Stratefy" method (Pierce et al., 2017). Regarding taxa that we were not able to sample, for 15 (3.1 %) taxa we employed CSR scores from close relative taxa in our dataset, while for 34 (7.3 %) taxa CSR scores were retrieved from databases (Chytrý et al., 2021; Pierce et al., 2017). The list of taxa for which CSR values were substituted from other morphologically similar taxa is given in Table S.1. 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 the species' CSR scores weighted by their square-rooted

relative abundance (Behroozian et al., 2020), by the *functcomp* function of the R package "FD" (Lavorel et al., 2008).

2.4. Environmental data

For the identification of the environmental conditions of communities, we used the Ecological Indicator Values (EIVs) for Europe (Dengler et al., 2023). Specifically, weighted mean indicator values for light, temperature, soil reaction, moisture and nutrient availability were calculated for each vegetation plot, by employing only taxa with three or more occurrences in the dataset. Subsequently, the weighted average indicator values for each plot were calculated as the average of the indicator values of all the taxa present in the plot, weighted by their abundance, raised to a power of 0.3 to reduce the effect of dominant species. For each taxon without an original indicator value, new values were estimated by calculating the average value of the five taxa with the highest fidelity (at least 20) to the taxon under question, using the JUICE software (Tichý, 2002). Additionally, a set of climatic, topographic and edaphic factors were employed in order to test the relation among functional plant strategies and environmental gradients. The initial dataset of climatic factors included the 19 bioclimatic variables available from the CHELSAcruts dataset (Karger et al., 2017), while after checking for autocorrelation among these variables, we selected only the annual precipitation, precipitation seasonality, annual temperature and temperature seasonality. The terrain's slope was used as a topographic factor, derived from the Copernicus Digital Elevation Model ("EU-DEM v1.1 — Copernicus Land Monitoring Service," n.d.), while the sum of total soil organic carbon, the total nitrogen and the pH at a depth of 0–5 cm (Poggio et al., 2021) were used as edaphic variables.

2.5. Statistical analyses

Vegetation classification of the 250 sampled vegetation plots was conducted after the exclusion of species with one or two occurrences in the dataset. Raw abundance values were standardized using the Hellinger method, which standardizes abundance by site and then applies a square-root transformation (Legendre and Gallagher, 2001). 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).

To quantify the extent of deviation between the observed pattern of functional strategies found in each community and random expectations, we calculated the standardized effect size (SES) for the C, S and R values. For each vegetation plot, 999 simulated assemblages were created by employing the "richness" null model of the "picante" package (Kembel et al., 2010) in R and the ses.C, ses.S and ses.R values were calculated according to the expression of standardized SES = [*observed – mean of null*] / *standard deviation 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.

For the investigation of taxonomic and functional diversity, we employed Hill numbers, which have been proposed as an appropriate approach for the calculation of abundance-based species diversity. Hill numbers constitute a set of indices differing only by a parameter that determines sensitivity to species relative abundances, named q (Hill, 1973; Jost, 2007, 2006). Within this parametric family of diversity indices, three widely used species diversity metrics are included, namely species richness corresponding to a $q = 0$, Shannon diversity when $q = 1$ and Simpson diversity when $q = 2$. Diversity profiles based on the accumulation of vegetation plots were created for $q = 0$, $q = 1$, $q = 2$ and $q = 8$, with interpolation/extrapolation analysis carried out with the R package "HillR" (Li, 2018).

For the assessment of diversity between communities, we calculated β diversity for all possible pairs of vegetation plots (Baselga, 2010). We used the Sørensen dissimilarity index to estimate the total β diversity

between vegetation plots, which was subsequently partitioned to turnover β diversity and nested β diversity. Turnover indicates the replacement of species between samples, while nestedness indicates the overall variation due to differences in richness between different samples (Baselga, 2010). The three metrics of β diversity were calculated for both taxonomic and functional aspects of diversity. Differences in species richness and composition were assessed for taxonomic β diversity and were calculated using the function *beta.pair* from the R package "betapart" (Baselga and Orme, 2012). Differences in plant functional strategies occurring within the communities were assessed for functional β diversity with the function *functional.beta.pair* from the R package "betapart" (Baselga and Orme, 2012).

The Spearman's correlation coefficient was used to quantify the relationships among the ses.C, ses.S and ses.R and the environmental variables employed in the present study, namely annual precipitation, precipitation seasonality, annual temperature and temperature seasonality, slope, sum of total soil organic carbon, the total nitrogen and the pH at a depth of 0–5 cm.

Finally, variation partitioning analysis was used to determine the effects of these environmental variables on species composition, as well as the effects of land use-cover change (see Section 2.2) on the CWM CSR scores of all vegetation plots. The analysis was conducted for all the sampled vegetation plots, and for grassland and forest vegetation plots separately, using the *varpart* function of the "vegan" package in R (Oksanen et al., 2022).

3. Results

3.1. Vegetation communities

We identified 11 distinct vegetation communities within our study area, namely six communities dominated by herbaceous species (hereafter referred as grasslands) and five forest communities (Table S.2, Table S.3). Furthermore, according to their composition in vegetation plots with different successional pattern and the contribution of expert judgment, when necessary, these communities were interpreted as representing different succession stages.

Herein, we provide a short description of the distinguished communities regarding their ecology and the succession stage they represent (Table S.2), while their floristic differentiation is presented in Table S.3, and their differentiation in terms of EIVs is illustrated in Fig. S.1. Six grassland communities were identified, and found to belong to four distinct succession stages. Specifically, hay meadows with *Alopecurus rendlei* community represent lowland hay meadows regularly mowed at least once a year (early summer), which, due to this annual disturbance, barely host any woody species. These vegetation plots were found to have high levels of moisture and nutrient availability compared to the rest of the grassland communities, as well as low levels of soil pH. *Hordeum bulbosum* community represents old fields of different years after the abandonment of their cultivation (2–3 to > 10 years). The establishment of woody species in this vegetation type is limited, due to regular grazing and/or irregular mowing, but in a few remote areas it is more advanced. This community develops on plain soils (former arable lands) rich in nutrients, but with moderate soil moisture. Hay meadows with *Alopecurus rendlei* and old fields with *Hordeum bulbosum* were identified to be at an early grassland succession stage. Mesic meadows with *Cynosurus cristatus* constitute a community under ongoing succession, caused by different intensities of periodic grazing leading to various levels of encroachment of woody species. This community was found to have similar ecological conditions with the old fields with *Hordeum bulbosum* but with lower nutrient availability. Mesic meadows with *Cynosurus cristatus* were identified to be at an ongoing grassland succession stage. *Chrysopogon gryllus* and *Phlomis fruticosa* communities constitute semi-natural grasslands representing a stable successional stage, submitted to frequent grazing. Specifically, the *Chrysopogon gryllus* community includes dry semi-natural grasslands occurring on

both acidic and basic substrate, whereas *Phlomis fruticosa* community represents semi-natural grassland-phryganic vegetation occurring on calcareous substrate. Both these communities develop on sites having more extreme conditions regarding soil nutrient and moisture content combined with warmer conditions, with the *Phlomis fruticosa* community occupying the most extreme sites. In these two communities, the succession proceeds very slowly due to the extreme soil and climatic conditions and for this reason they are herein characterized as being at an advanced stable grassland succession stage (it should be noted that *Phlomis fruticosa* community it was found to occur in all of its sampling localities since 1945).. *Pteridium aquilinum* community possibly constitutes a retrogressive succession stage after the destruction of forests on acidic substrates, dominated by dense thickets of bracken in large openings of forests or in areas adjacent to forests, with a restricted distribution in the study area.

Regarding the forest communities, *Carpinus orientalis* forests and xero-thermophytic oak forests constitute two successionally stable communities that are subjected to medium disturbances due to activities of animal husbandry (e.g., low-intensity grazing, resting of livestock) and are, to some extent, possibly related to historical legacies of past land uses and management, such as cultivation on steep slopes or fire management for maintaining grasslands. Such management regimes possibly led to the degradation of soil, enhancing soil erosion. More specifically, the *Carpinus orientalis* community is a paraclimax forest vegetation type, replacing the climax vegetation type on soils degraded by human use, which are usually shallow and rocky, on steep slopes, but with adequate water supply. Xero-thermophytic oak forests represent oak forests dominated mainly by *Quercus trojana, Q. coccifera* or *Q. pubescens*, growing on drier and warmer sites than the rest of the forest communities. *Carpinus orientalis* forests and xero-thermophytic oak forests are herein considered as being at an advanced stable forest succession stage. Moreover, two forest communities were found at late

succession stages, submitted to relatively limited logging. The first one is the *Quercus frainetto* community, which constitutes the climax forest vegetation of the study area, occurring mainly on acidic, relatively deep and rich in nutrients soils. The second is the *Quercus cerris – Q. frainetto* community, which is a variant of the climax forest community in the area, occurring on more base-rich soils. The latter two communities were identified to be at a late forest succession stage. Finally, riparian forests of *Alnus glutinosa* or *Platanus orientalis*, also identified to be at a late forest succession stage, are growing along streams at the lowland part of the study area, representing remnants of once extensive plain riparian forests. Despite the lack of prevalent differences regarding current disturbances on forest communities, we may hypothesize that these differ based on their past disturbance regimes, depending on the type of past land use and the intensity of past disturbances.

3.2. Functional diversity of CSR scores

Our dataset included 457 taxa with available information of functional traits, occurring in more than two sampled vegetation plots. These taxa were assigned to all 19 available ecological strategies, with the two mainly occurring life strategies being S/SR and SR. At the vegetation plot level, the CWM CSR scores had a much more restricted distribution across the CSR triangle (Fig. 2). Grassland communities had clearly differentiated functional strategy spectra from forest communities, and were characterized by higher levels of stress and disturbance and lower levels of competition compared to forests (Fig. 3, Fig. 4).

CSR scores varied significantly among the identified vegetation communities (Fig. 3, Fig. 4), although most communities included taxa classified to all 19 ecological strategies according to the CSR approach (with the exception of four communities which included taxa classified to 17 and 18 ecological strategies). Differentiation of communities was to a large extent clear for both grassland and forest communities. The
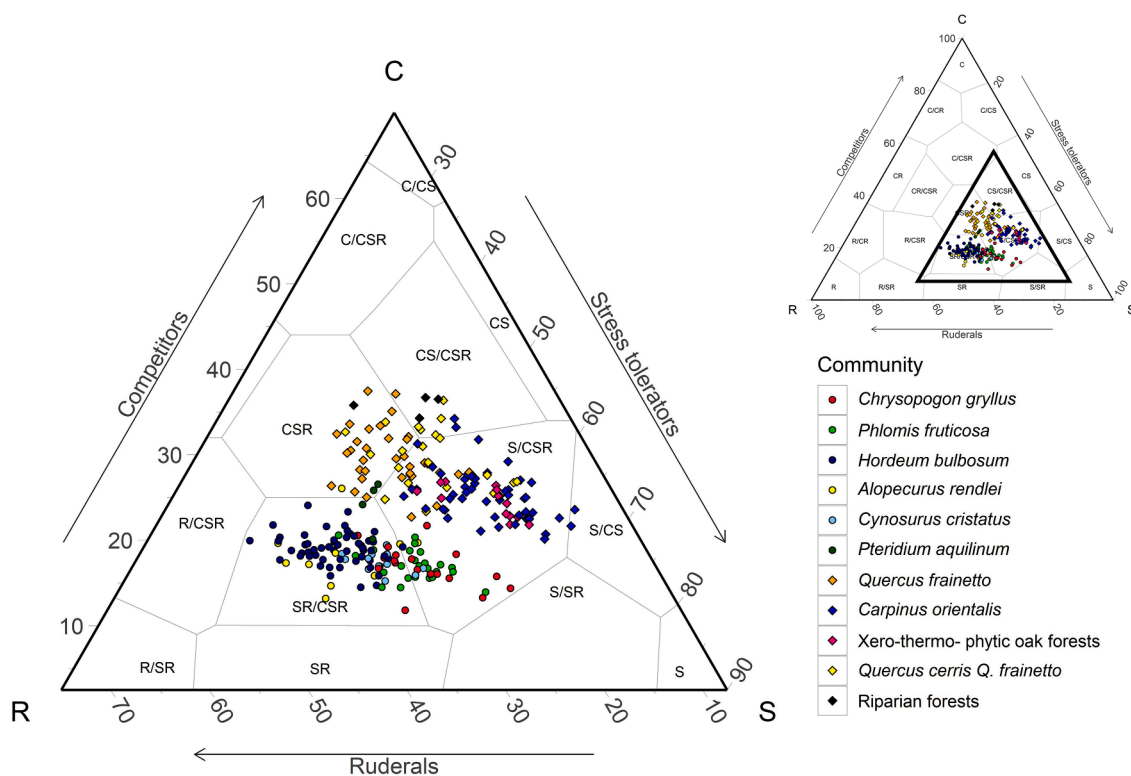

Fig. 2. Close-up view of the distribution of the CWM CSR scores in a ternary plot (i.e. CSR triangle in the top right inset) among the different communities. The C, S and R represent the components of competitive, stress tolerating and ruderal functional strategies in CSR triangle, respectively. Grassland vegetation plots are represented by filled circles and forest plots by filled diamonds. Color fill represents the different communities within grasslands and forests. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
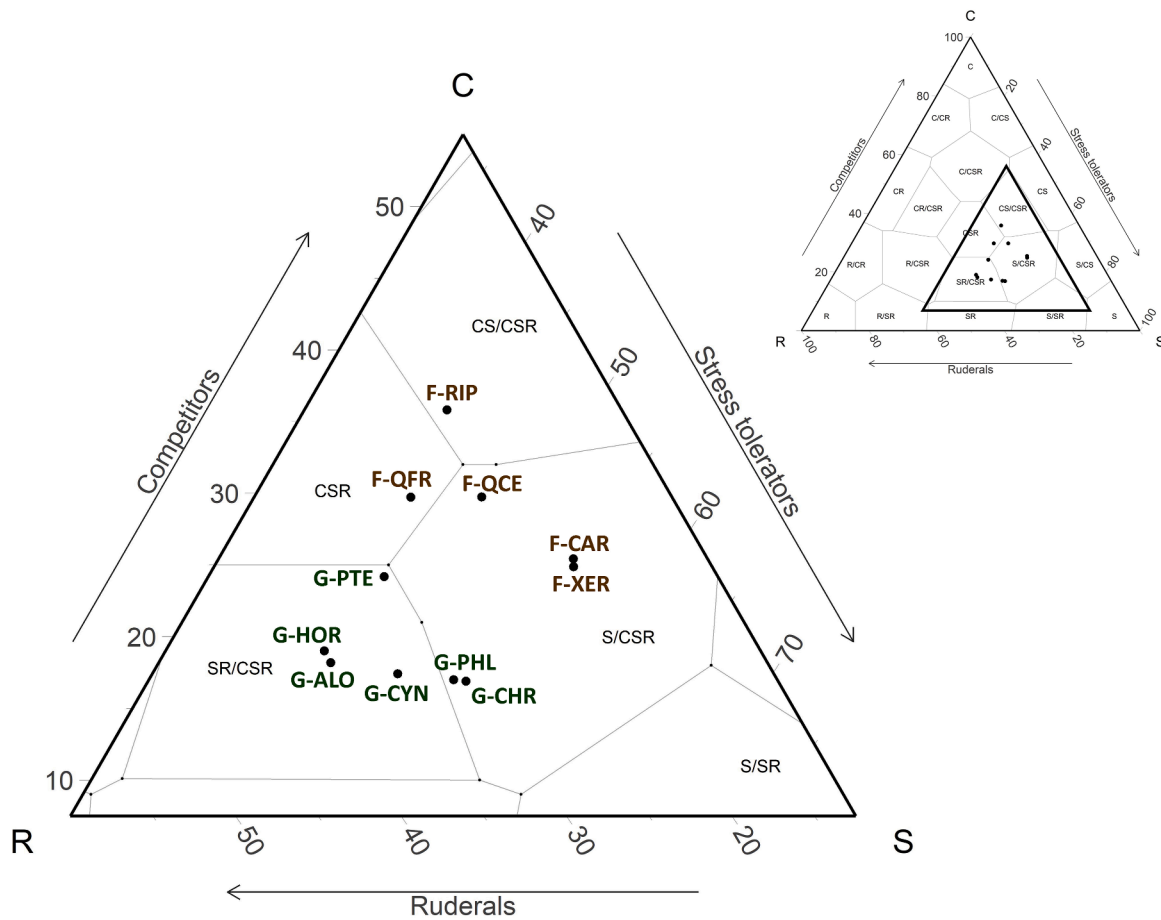
Fig. 3. Close-up view of the distribution of the community level CSR scores in a ternary plot (i.e. CSR triangle in the top right inset). The C, S and R represent the components of competitive, stress tolerating and ruderal functional strategies in CSR triangle, respectively. Grassland communities (green font): hay meadows with Alopecurus rendlei (G-ALO), Hordeum bulbosum community (G-HOR), mesic meadows with Cynosurus cristatus (G-CYN), Chrysopogon gryllus community (G-CHR), Phlomis fruticosa community (G-PHL) and Pteridium aquilinum community (G-PTE). Forest communities (brown font): Carpinus orientalis community (F-CAR), xero-thermophytic oak forests (F-XER), Quercus frainetto community (F-QFR), Quercus cerris – Q. frainetto community (F-QCE) and riparian forests of Alnus glutinosa or Platanus orientalis (F-RIP.).
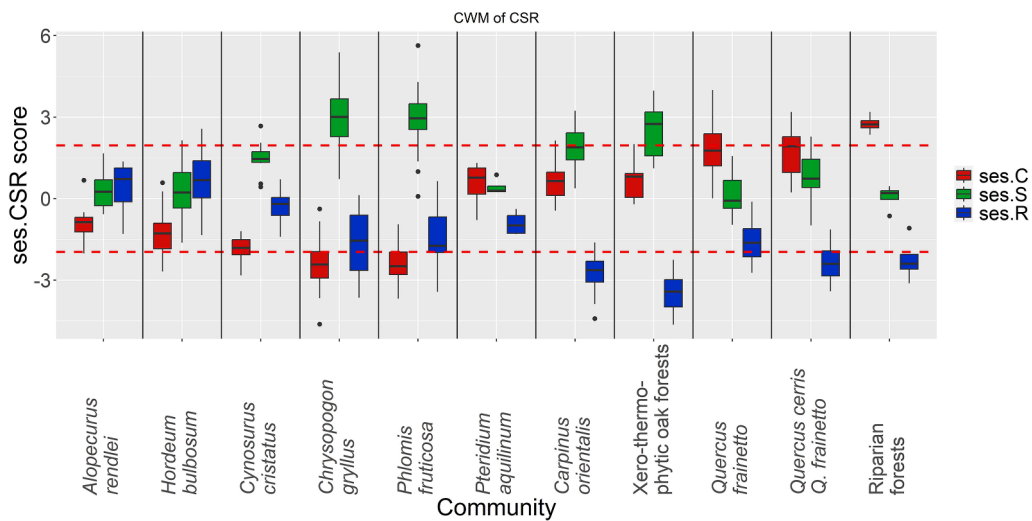

Fig. 4. Standardized effect sizes of the competitive (ses.C), stress tolerating (ses.S) and ruderal (ses.R) functional strategies among vegetation communities. The order of vegetation communities represents the successional gradient found in the present study, from the early grassland successional communities (left) towards the late forest succession communities (right). Values < −1.96 indicate significant functional clustering, whereas values > 1.96 indicate significant functional over-dispersion (according to the "richness" null model). The threshold values are indicated by the dashed horizontal lines. The box plots show the medians (black horizontal lines in the 25th–75th percentile boxes), and the outliers (black dots).

advanced stable semi-natural grassland communities with *Chrysopogon gryllus* and *Phlomis fruticosa* had statistically significant lower levels of the competitive functional strategy and statistically significant higher levels of the stress tolerating strategy (Figs. 3 and 4). The functional strategies observed for the communities of old-fields with *Hordeum bulbosum*, hay meadows with *Alopecurus rendlei* and wet meadows with *Cynosurus cristatus*, although did not differ from random expectations based on their species richness (Fig. 4), they were observed to have distinct patterns (Fig. S.2). Similarly to the first two communities, the plots of these communities were characterized by low levels of the competitive strategy. The two communities of early grassland succession stages, namely old-fields with *Hordeum bulbosum* and hay meadows with *Alopecurus rendlei*, had very similar patterns of functional strategies, with stress tolerating and disturbance strategies being equally represented, while in wet meadows with *Cynosurus cristatus*, identified to be at an ongoing grassland succession stage, a trend of higher levels of stress tolerating and lower disturbance strategies was observed.

In the successionally retrogressive vegetation plots of the *Pteridium aquilinum* stands, the functional strategies were found to be in transitional levels between grassland and forest communities. Forests were found to be grouped in two subgroups of communities with similar functional strategies, similarly to the groups that occurred based on their ecological differentiation. Specifically, the more mesic and late successional forest communities (*Quercus frainetto* forests and *Quercus cerris – Q. frainetto* mixed forests) were characterized by statistically significant higher levels of competition and lower levels of stress tolerance and disturbance. In contrast, the communities of an advanced stable forest succession stage, including the more xero-thermophytic communities (*Carpinus orientalis* forests and Xero-thermophytic oak forests with *Quercus pubescens – Q. trojana*), had statistically significant higher level of stress tolerance and statistically significant low level of disturbance (Fig. 4). Riparian communities were more similar to the mesic forest communities of *Quercus frainetto* and *Quercus cerris – Q. frainetto*, but exhibiting an even more clear trend of statistically significant higher level of competitive species and simultaneously lower level of ruderal species.
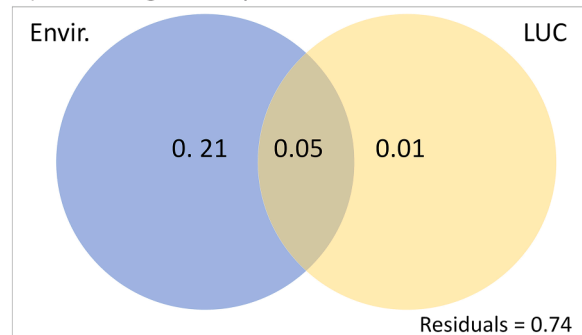
Variation partitioning on the basis of CWM CSR scores revealed that patterns of land use change (Fig. 5) represent succession paths in our study area. In total, land use, climatic, soil and topographic variables explained a particularly high percentage of the observed variation in CWM CSR scores of vegetation communities (57 % of total variation). The same variables explained lower levels of variation when grassland and forest vegetation communities were investigated separately, with the total explained variation reaching 28 % for grasslands and 26 % for forests. Land use change explained 34 % of the variation in CSR scores when all vegetation plots were simultaneously used, and 10 % of the variation in CSR scores of the grassland vegetation plots, but only 1 % of the variation of the forest vegetation plots. On the contrary, the employed climatic, edaphic and topographic variables were found to explain the highest levels of the variation in CSR scores (21 %) for the forest vegetation plots, but only 9 % of the variation for grasslands and all vegetation plots. The respective results for the species diversity are presented as Supplementary material (Fig. S.3). Although they are in agreement with the results derived from the CWM CSR scores, the total amount of explained variation is lower, reaching 24 % for the dataset of all plots. The amount of variation explained by land use changes remains higher than that explained by environmental variables for the dataset of all plots and grasslands, although for grasslands the explained variation is somewhat lower than it is for all plots. Finally, for forests, the amount of variation explained by land use changes is very small compared with variation explained by the environmental variables.

From the investigation of correlations between ses.C, ses.S and ses.R values of vegetation plots and climatic variables, edaphic factors and slope, the latter two types of variables were found to be more strongly correlated with the observed functional strategies (Table 1). Specifically, slope, soil organic carbon, nitrogen and pH were found to have
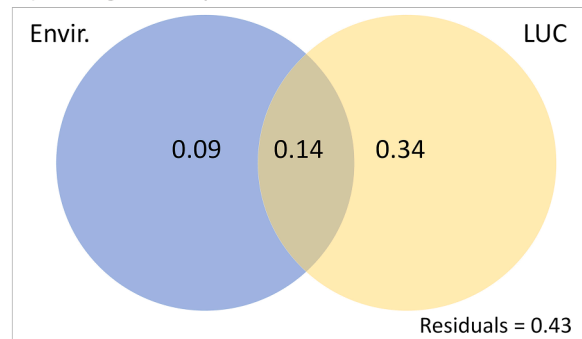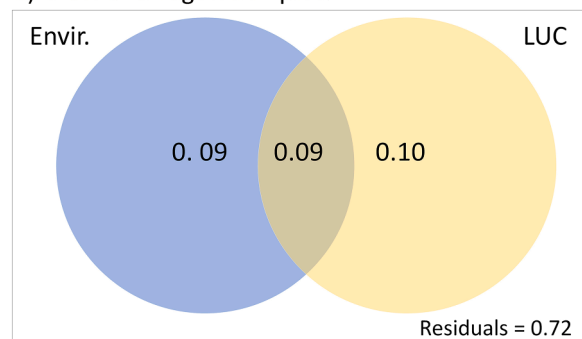

Fig. 5. Variation partitioning analysis for the effects of environmental variables (Envir.: slope, annual precipitation, precipitation seasonality, annual temperature, temperature seasonality, soil organic carbon, total nitrogen and pH at depth of 0–5 cm) and land use change (LUC) between years of mapping (1945, 1970, 1996, 2015) on the CWM CSR scores of: (A) all vegetation plots; (B) forest vegetation plots; and (C) grassland vegetation plots. The unique effect of a partition for each variable appears in the corresponding non-overlapping portion of each circle. The cross sections represent co-influence, while Residuals are the unexplained part. Note that the size of the circles is not correlated with the variance explained.

statistically significant and strong correlation with the observed functional strategies, while the four climatic variables had only few statistically significant correlations with the ses.C, ses.S and ses.R values which were not particularly strong. Statistically significant higher levels of competitive plant functional strategy were positively correlated with high soil content in organic carbon and nitrogen as well as with lower pH values. In contrast, statistically significant higher levels of the stress tolerating plant functional strategy were observed in habitats with lower soil content in organic carbon and nitrogen as well as in higher pH values. Finally, steeper slopes supported statistically significantly lower levels of plant functional strategies related to disturbance.

Table 1
Spearman's correlation coefficients between standardized effect sizes of the competitive (ses.C), stress tolerating (ses.S) and ruderal (ses.R) functional strategies and the topographic (slope), edaphic (soil organic carbon, nitrogen and pH) and climatic variables (annual prec: annual precipitation, prec season: precipitation seasonality, annual temp: annual temperature and temp season: temperature seasonality). Statistical significance of correlations between ses.C, ses.S and ses.R and the predictor variables was calculated for all vegetation plots, as well as from forest and grassland vegetation plots separately. (and associated p-values, ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$).

	Vegetation type	Slope	Soil organic carbon	Nitrogen	pH	Annual Prec	Prec Season	Annual Temp	Temp Season
ses.C	overall	0.139*	0.484***	0.384***	−0.406***	0.115	0.183**	−0.033	−0.183**
	forest	0.204*	0.335***	0.219*	−0.349***	0.365***	0.166	−0.270**	−0.312***
	grassland	0.095*	0.354***	0.297***	−0.187*	0.059	0.215*	−0.028	−0.163
ses.S	overall	0.311***	−0.190**	−0.261***	0.255***	0.065	−0.206**	−0.058	0.085
	forest	0.0283**	−0.120	−0.325***	0.371***	0.022	−0.272**	0.059	0.144
	grassland	0.329***	−0.126	−0.141	0.060	0.048	−0.120	−0.075	0.044
ses.R	overall	−0.429***	−0.241***	−0.082	0.099	−0.168**	0.034	0.076	0.102
	forest	−0.493***	−0.145	0.137	−0.151	−0.360***	0.143	0.166	0.091
	grassland	−0.415***	−0.109	−0.060	0.064	−0.092	−0.014	0.093	0.090

3.3. Taxonomic and functional diversity

Taxonomic diversity of grassland communities was consistently higher than diversity of forest communities, across all levels of the q parameter, with the only exception of the community of hay meadows with *Alopecurus rendlei* (Fig. S.4). The communities with the highest levels of taxonomic diversity were the two advanced stable grassland communities with *Chrysopogon gryllus* and *Phlomis fruticosa*, while hay meadows with *Alopecurus rendlei* at the early grassland succession stage had the lowest diversity levels. The hierarchy of communities based on their taxonomic diversity does not change with the alteration of the metric's sensitivity to species relative abundances. Similar is the observed pattern for the functional diversity, but it should be noted that the difference between grassland and forest communities is greater based on Hill numbers of functional diversity, since grasslands and forests have more similar levels of effective number of species based on taxonomic rather than functional diversity (Figs. S.4 and S.5). Additionally, based on the total functional Hill numbers, greater unevenness (steeper slopes) of functional diversity was observed in grassland communities than in forests (Figs. S.4 and S.5).

Regarding beta diversity, the derived results differed significantly between the taxonomic and functional aspect of diversity. The overall taxonomic beta diversity among communities was significantly greater than the overall functional beta diversity (Fig. 5). Turnover was the main component of taxonomic beta diversity and it was higher between grasslands and forest communities. On one hand, taxonomic nestedness was significantly lower and its greater values were observed among the forest communities (Fig. S.6). On the other hand, nestedness was the main component of the functional aspect of beta diversity, with higher values mostly among grassland and forest communities (Fig. S.6). For both taxonomic and functional beta diversity, hay meadows with *Alopecurus rendlei* were found to have distinct patterns of diversity. Specifically, we observed particularly high values of taxonomic and functional turnover between this community and the *Pteridium aquilinum* community and all forest communities, as well as high values of functional nestedness between this community and the seminatural grasslands with *Chrysopogon gryllus* and *Phlomis fruticosa* and old-fields with *Hordeum bulbosum* (Fig. 6).

4. Discussion

4.1. Community-level CSR strategies between general vegetation types and among communities

The investigated landscape was found to host six grassland communities and five forest communities, representing distinct stages of secondary succession, as a result of the historical and ongoing phenomena of land use changes in the study area (Kiziridis et al., 2022). These ecologically well-differentiated communities were characterized by greater taxonomic variability and they were clearly found to be functionally differentiated, according to Grime's CSR model.

A particularly high level of differentiation, both taxonomic and functional, between vegetation communities was explained mainly by the effects of land use cover. It is indicated that differences between the two main vegetation types, namely open vegetation (grasslands and shrubland) and forests are governed mainly by current as well as historical human induced disturbances. Therefore, succession is linked to the diversity of CSR functional strategies in plant communities, confirming the expected replacement of early establishing ruderal colonizers by more competitive or more stress-tolerant species (Caccianiga
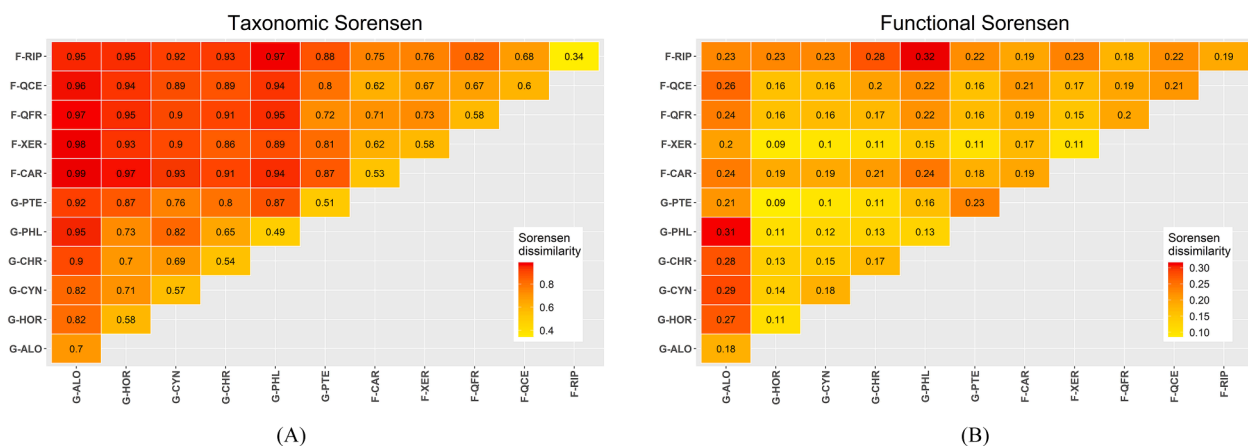

Fig. 6. Heatmaps of cross-correlating taxonomic (A) and functional (B) β diversity between vegetation communities. For abbreviations of communities please see the caption of Fig. 3.

et al., 2006), depending also on the stage and trajectory of succession based on the existing biotic and abiotic conditions. Loranger et al. (2016) recently demonstrated that early and late successional stages are less functionally diverse than middle successional stages, due to the interchangeable importance of processes such as environmental filtering and competitive exclusion during succession. Our results are partly in agreement with this general concept. More specifically, in communities of advanced but stable grassland succession stage and late forest successional stage, we observed statistically significant higher levels of the stress-tolerating or competitive strategy, respectively. In contrast, in communities under advanced ongoing succession stage but also at early grassland succession stage did not differ from random expectations regarding their composition in stress-tolerating, ruderal or competitive species, implying a higher diversity in these communities.

Diversity of functional strategies in plant communities have been found to change along succession, with many studies recording increasing stress-tolerance and decreasing ruderality during secondary succession of grassland communities (Kelemen et al., 2017; Navas et al., 2010; Prévosto et al., 2011; Zanzottera et al., 2020). Respectively, decrease of the CWM values of stress tolerance or abundance of stress tolerance taxa and increase of CWM values of competition or abundance of competitive taxa has been observed during secondary succession of forest ecosystems, such as tropical rainforest communities, lowland ombrophilous forests as well as European mixed pine-beech forests (Chen et al., 2022; Curt et al., 2003; Silva et al., 2015). Our results are not only in agreement with these patterns of CSR strategies, but they also allow greater generalizations regarding the interchangeability of functional strategies during succession, since our study is based on data from communities ranging from pioneer to stable stages of succession. Particularly, we have interestingly observed a correspondence of functional diversity patterns between grasslands and forests separately, for all the three CSR strategies. We found two communities that occur at extreme environmental conditions and being dominated by stress tolerators in both grasslands (*Chrysopogon gryllus* and *Phlomis fruticosa*) and forests (*Carpinus orientalis* and xero-thermophytic oak forests). Similarly, in both grasslands and forests there are communities which are characterized by environmental conditions or disturbance regimes that favor the abundance of either competitors or ruderal species, albeit that the former are clearly more abundant in forests and the latter in grasslands.. Regarding the ruderal strategy, although lower for all forest communities, a correspondence between grassland and forest communities was also prevalent, since the abovementioned grasslands and forests, with high values of stress tolerating strategy, were also found to have the lowest CWM values of the ruderal strategy. Concerning the life strategy of competition, this was more prevalent in the more mesic forest and grassland communities. Therefore, similar patterns of the quantitative distribution of plant life strategies were observed between the two general types of vegetation which are mainly formed due to present and past disturbance regimes.

The results of β diversity analyses further support the conclusion that parallel trends of CSR strategies are observed in both grassland and forest communities, since there is available niche space that can host most of the plant life strategies. Dissimilarity between communities was much greater than dissimilarity within each community for taxonomic but not for functional diversity, with exception being only hay-meadows and riparian forests. Furthermore, hay-meadows were found to have particular patterns of diversity, since they were functionally more similar to forest communities rather than the rest of the grassland communities. This can be attributed to the differences in disturbance regime of these communities, since all grasslands are submitted to grazing but hay-meadows are also submitted to other management practices such as mowing. Therefore, grazing causes reduction of interspecific competition in these communities through selective disturbance, favoring plant traits linked to herbivory resistance strategies (Davies, 2001; Díaz et al., 2007), while mowing constitutes a non-selective type of disturbance which allows plants to complete their reproductive cycle, leading to a more complex trait-determined use of different temporal reproductive niches (Catorci et al., 2012; Köhler et al., 2005). Grazing and mowing, which were the main varying forms of disturbance regimes among the studied communities, have been previously found to be important drivers of vegetation structure and community composition leading to prevalence of the ruderal functional strategy (Caccianiga et al., 2006; Pierce et al., 2007).

4.2. Community-level CSR strategies in relation to environmental factors

Soil factors were found to affect the patterns of prevalence among the three life strategies in the vegetation communities of our study area. More specifically, community-level functional diversity of vegetation plots was more strongly correlated to soil organic content, soil nitrogen, soil pH and slope. The abovementioned soil characteristics were considered the main drivers of the functional differentiation between grassland and forest communities in the present study, but also within each major vegetation type (i.e., grasslands and forests). Confirming the expectation of unproductive habitats favoring functionally stress tolerating species (Chapin et al., 1993; Grime et al., 1997), the stress-tolerating strategy was more prevalent in communities observed in habitats with lower soil organic carbon, lower nitrogen and higher pH. On the contrary, competitive strategy was more prevalent under the opposite conditions, as it has been previously highlighted in habitats with higher resource availability where plants are allowed to invest more in growth and rapid uptake of resources, leading to prevalence of the competitive functional strategy (Negreiros et al., 2014; Pierce et al., 2017). Overall, life strategies are expected to change from a pattern of conservation of resources in poor environments to further nutrient exploitation in environments richer in resources (Semchenko et al., 2018). Additionally, soil pH affects soil nutrient availability, microbial activity, and therefore plant functional diversity (Ma et al., 2021), which may indirectly affect the CSR strategies of plants (Yu et al., 2022). Particularly, habitats with soils of significantly low or high pH can also pose limiting factors for plant growth due to associated low availabilities of nutrients such as phosphorus and iron (Bartelheimer and Poschlod, 2016; Behroozian et al., 2020).

Although some statistically significant correlations were observed among climatic factors and the functional strategies for the vegetation plots within our study area, these were not particularly strong. Annual precipitation was found to have the strongest effect on functional strategies among the investigated climatic variables, with the competitive strategy being positively affected by higher levels of annual precipitation, especially for forest communities, opposite to the ruderal strategy. Overall, the positive correlation of annual precipitation and negative correlation of temperature seasonality with the competitive functional strategy, observed at a local scale within our study area, is in agreement with the observed relations among climatic variables and functional strategies at a global scale (Pierce et al., 2017). Water availability and temperature are considered among the main determinants of plant survival and distribution, while low precipitation levels as well as high temperature seasonality constitute important stressors of plants. More or less, the same type of correlations between CWMs and environmental factors with those described above can be concluded by comparing the standardized effect sizes of CWM CSR values with the community level EIVs. The more important role of soil and physiographic variables than the climatic ones in determining the life strategy of plant species in the communities, should be considered as expected due to the local scale of our study. Particularly, several studies have shown that soil, physiographic and microclimatic differentiation are the main drivers of floristic and functional differentiation of vegetation at a local scale (Fortin and Dale, 2005; Han et al., 2020; Knollová and Chytrý, 2004).

4.3. Implication for conservation

The importance of abandonment of agricultural land on biodiversity

is particularly prominent in Europe, since it is estimated that 50 % of all species in Europe, including a number of endemic and threatened ones, depend on agricultural habitats (Kristensen, 2003). Such habitats, including livestock, arable or mixed farming systems, usually rely on traditional low intensity practices (Doorn and Elbersen, 2012; Pedroli et al., 2007). Such High Nature Value Farmland (Baldock et al., 1993; Beaufoy et al., 1994) is typically characterized by a combination of low intensity land use, the occurrence of semi-natural vegetation and unfarmed regions and a diversity of land cover and land uses (Beaufoy and Cooper, 2008). Our study area used to constitute such a dynamic and greatly heterogeneous landscape, formed by a number of traditional management practices, including livestock grazing, mowing and burning, similar to several European mountainous regions (Valkó et al., 2018). Nevertheless, during the last 70 years, these traditional activities have been significantly reduced, and a very high percentage of ex-arable land has converted to forest vegetation through natural revegetation (Kiziridis et al., 2022). Several studies have demonstrated that such a reduction of landscape heterogeneity after land abandonment is possible to have significant effects on biodiversity, both negative (e.g. biodiversity decline) or positive (e.g. opportunity for regeneration of native ecosystems) (Queiroz et al., 2014).

Despite the central role that taxonomic diversity has played historically in the biodiversity monitoring and conservation planning, the crucial role of functional diversity in achieving biological conservation goals is becoming particularly prevalent during the last decade (Aquilué et al., 2021; Cadotte, 2011; Cadotte et al., 2011). Specifically, functional diversity as well as functional redundancy of communities are considered highly related to ecosystem resilience, thus allowing comparisons across different ecosystems, regions and management systems, and capturing effects of disturbance (Lelli et al., 2019). Our findings, and especially results derived from β diversity analyses, strongly support the particularly important and complementary role of functional diversity on decision making throughout conservation planning. Although α taxonomic and functional diversity allows similar conclusions regarding the differentiation of diversity patterns between communities, functional β diversity provides more information about differentiation between communities, as well as about functional redundancy within and among communities.

Specifically, functional β diversity was more informative about the differentiation patterns within and between the general vegetation types. Functional differentiation was again higher between grassland and forest communities, with semi-natural grassland with *Phlomis fruticosa*, hay-meadows with *Alopecurus rendlei, Carpinus orientalis* forests, *Quercus cerris – Q. frainetto* mixed forests and riparian forests having higher functional beta diversity than the rest of the communities, attributed mainly to functional nestedness. Therefore, the higher taxonomic and functional α diversity of grassland communities indicates that functional diversity of forests constitutes to a great extent a fraction of the diversity occurring in grassland communities. Additionally, the high taxonomic β diversity between grassland and forest communities indicates that many species of grassland habitats are going to be extinct from the area if the afforestation through natural succession will not be halted.

Kiziridis et al. (2023) found for our study area that if the present trend of land abandonment and the subsequent secondary succession continues, in 2055 the forests will increase to 79 % of the total area (from 62.6 % in 2015), the farmland will decrease to a critical 0.4 % (from 3.2 % in 2015) and the more or less open habitats (grasslands and open scrubs) will comprise less than 12.4 % of the total area (from 23 %). On the one hand, this means that some species may become extinct, while some others will face a significant decrease of their population. On the other hand, in terms of life strategies, the reduction of diversity will possibly be less significant, as stress tolerators exist in both grassland and forest communities, and the rest two strategies are also well represented in some communities of both main vegetation types. Interestingly, the two communities of *Alopecurus rendlei* and of the riparian

forests, which were found to have a more unique functional signature (higher functional beta diversity in comparison with the rest communities), are the poorest communities in terms of taxonomic and functional α diversity.

Combined with the extremely high level of afforestation after abandonment of arable land within our study area (Kiziridis et al., 2023, 2022), it is becoming prevalent that systematic conservation planning and management through support and regulation of appropriate agricultural activities is crucial for biodiversity conservation in such rapidly changing ecosystems. Specifically, identification of such patterns can improve our understudying regarding the management practices that should be ceased, maintained or even intensified, in order to achieve conservation goals, by exploiting the effects of disturbances such as grazing, mowing or burning on the communities' functional diversity (Kahmen et al., 2002). Additionally, functional diversity and uniqueness can assist conservation and lead to the improvement of conservation outcomes (Violle et al., 2017), while they can also be employed for the evaluation of functional responses to already existing restoration projects (D'Astous et al., 2013; Hedberg et al., 2013).

Author contributions

IT coordinated the study; AM 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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CRediT authorship contribution statement

Anna Mastrogianni: Conceptualization, Investigation, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Diogenis A. Kiziridis:** Writing – review & editing. **Elpida Karadimou:** Investigation, Writing – review & editing. **Magdalini Pleniou:** Investigation, Writing – review & editing. **Fotios Xystrakis:** Investigation, Writing – review & editing. **Spyros Tsiftsis:** Investigation, Writing – review & editing. **Ioannis Tsiripidis:** Conceptualization, Investigation, Data curation, Methodology, Supervision, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.flora.2023.152399.

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