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Decoupled phylogenetic and functional diversity in European grasslands

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Abstract. The relationship between phylogenetic diversity (PD) and functional diversity (FD) is important for understanding the mechanisms of community assembly. The traditional view assumes a coupled (positively correlated) relationship between these two diversity measures, suggesting that competitive exclusion and environmental filtering are important drivers of both phylogenetic and functional structure of communities. In contrast, there is evidence that communities might deviate from this pattern, exhibiting either phylogenetic overdispersion connected with trait convergence (decoupled PD) or functional overdispersion connected with phylogenetic clustering (decoupled FD). In this study, we examined the relationship between PD and FD within vascular-plant communities in European grasslands, focusing on decoupled PD-FD patterns. We hypothesized that the decoupled patterns are connected with past or current environmental changes and are rarer in comparison with the coupled PD-FD pattern, reflecting long-term relatively stable environments. We used 81,484 plots (communities) of European dry, mesic, wet and alpine grasslands, containing 4,119 angiosperm species, and data on six functional traits relevant for different plant functions and habitats (plant height, leaf area, specific leaf area, leaf nitrogen content, seed mass and lateral spreading distance). Functional diversity was evaluated in two ways – as a single combined measure and as variability in each trait separately. We found various PD-FD patterns across different habitats, traits and regions, with the coupled pattern widespread but not universal. In many communities, we detected the tendency towards decoupled PD, likely caused by environmental filtering of phylogenetically diverse species pools. This was most pronounced in dry grasslands, and also in wet and alpine grasslands when FD based on plant height, leaf area or seed mass was considered. In contrast, the tendency towards decoupled FD was detected only in mesic and wet grasslands for leaf nitrogen content and lateral spreading distance, possibly due to competitive interactions among species interplaying with land-use history. Decoupled PD is relatively common in European grasslands, especially in mountainous and hilly areas of central and southern Europe and in parts of western Europe with a mild climate. This likely results from refugial effects that have preserved many distinct phylogenetic lineages, but their species are functionally similar due to environmental filters that affect the assembly of present-day grassland communities. We demonstrate that PD and FD may reflect different aspects of community structure and assembly mechanisms, and suggest that the phenomenon of decoupled PD and FD deserves more systematic study.

Keywords: angiosperms, biogeographic history, community assembly, Europe, functional diversity, functional trait, grassland, non-equilibrium process, phylogenetic diversity

Introduction

Broad-scale patterns of phylogenetic diversity (PD; Faith 1992, Webb 2000) and functional diversity (FD; Petchey & Gaston 2006, Díaz et al. 2016) provide insights into community assembly processes at different scales (Cavender-Bares et al. 2009, Baraloto et al. 2012, Prinzing 2016). While PD characterizes evolutionary distances between species, FD reflects differences in species trait values within the functional trait space. PD is used to understand the evolutionary and biogeographic histories of various communities (Ndiribe et al. 2013, Lososová et al. 2015, Prinzing 2016), while FD is used to study trait-environment relationships (Petchey & Gaston 2006, Lavorel et al. 2011). The relationship between PD and FD in ecological communities has been extensively debated (e.g. Bernard-Verdier et al. 2013, Pavoine et al. 2013, Dainese et al. 2015, Cadotte et al. 2019, E-Vojtkó et al. 2023). The traditional view assumes that increasing PD should be reflected in increasing FD and conversely, species with similar traits should be on average phylogenetically more related (coupled PD-FD pattern, Fig. 1A; Webb et al. 2002, Cadotte et al. 2013, de Bello et al. 2017). This paradigm (hereafter referred to as the ‘competitive exclusion – environmental filtering paradigm’) assumes that communities within a space defined by PD and FD axes should be positioned along a gradient that spans between phylogenetic and functional (i) overdispersion, associated with competitive exclusion preventing the coexistence of ecologically similar and phylogenetically closely related species (Fig. 1A, sector I; Darwin 1859, Elton 1946, Hutchinson 1959, MacArthur & Levins 1967); and (ii) clustering, associated with environmental filtering and habitat-dependent competition selecting for species that are closely related and functionally similar to each other (Fig. 1A, sector II; Williams 1964, Grime 1973, Keddy 1992, Webb 2000). It has been suggested that these two opposing situations can complement each other depending on the varying importance of competition or filtering by the environment along environmental gradients and across different spatial scales (Weiher & Keddy 1995, Cavender-Bares et al. 2004, Pausas & Lamont 2018).

While ecological literature is replete with studies that document coupled PD-FD patterns in plant communities (e.g. Prinzing et al. 2001, Swenson et al. 2007, Cavender-Bares et al. 2009, Gerhold et al. 2015, Cadotte et al. 2019), there are also studies that report different PD-FD patterns observed in assemblages of various organisms across diverse environmental and spatial settings (e.g. Cavender-Bares et al. 2004, Prinzing et al. 2008, Shafquat et al. 2014, Ding et al. 2021, Nicholson et al. 2023). Some results of these studies indicate that phylogenetic and functional structure of communities can also markedly deviate from the positive relationship between PD and FD (hereafter called decoupled PD-FD patterns, Fig. 1B). In such cases, the assembly of local communities has been proposed to arise from the interplay of historical processes, such as the (co)evolution of species traits and biogeographic dispersal (e.g. Fischer 1960, Ricklefs 1987, Wiens et al. 2011), with local environmental and biotic conditions (Prinzing et al. 2008, Cavender-Bares et al. 2009).

The classic Darwinian assumption of stronger competition among closely related species, leading to their mutual exclusion in communities (Fig. 1A, sector I), has been investigated in numerous studies yielding mixed results and generally weak empirical support, particularly for plants (Jarvinen 1982, Mayfield & Levine 2010). For example, Cahill et al. (2008) in their meta-analysis of competition experiments with vascular plants found

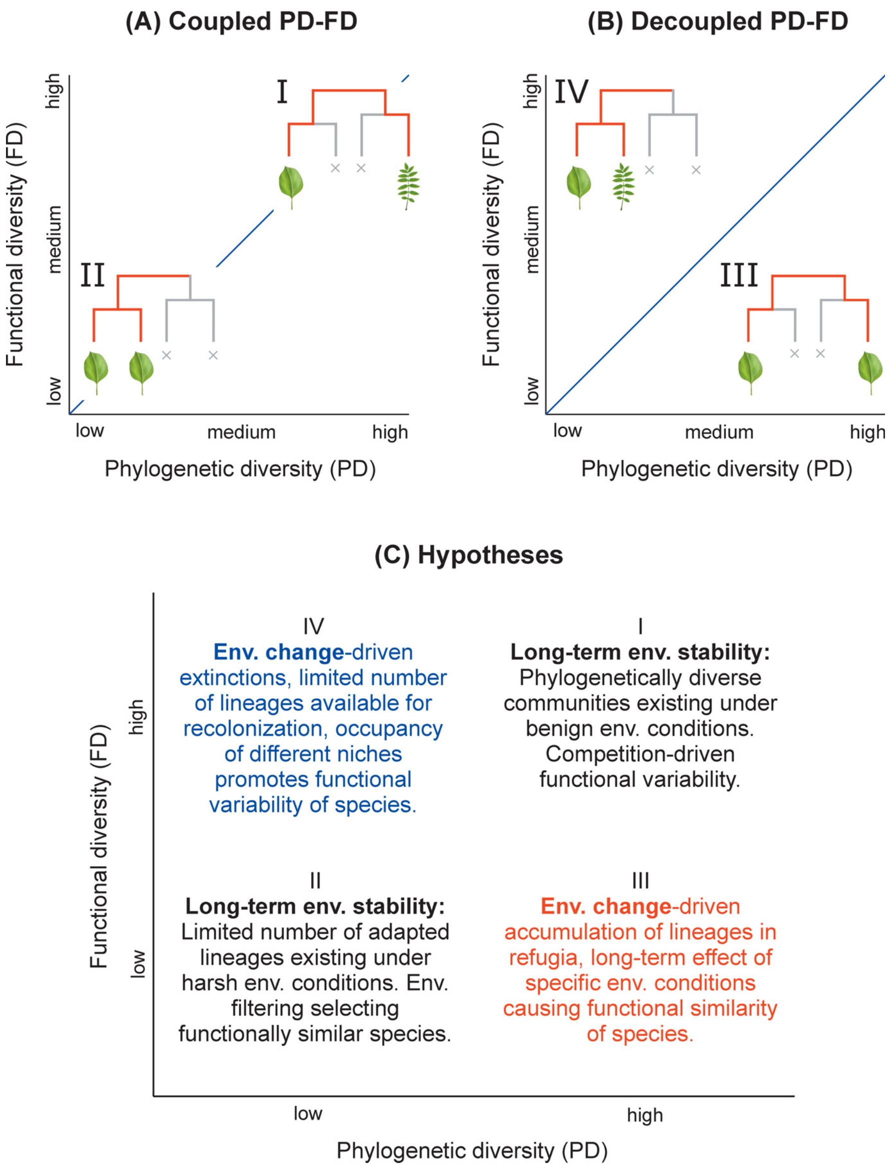


Fig. 1. Theoretical relationships between phylogenetic diversity (PD) and functional diversity (FD) in ecological communities: (A) Coupled PD-FD pattern reflects an expectation that phylogenetically closely related species within a community should be functionally more similar than distantly related species. Under this traditional perspective, the patterns of PD and FD consistently range from (I) overdispersed communities due to prevailing competitive exclusion to (II) clustered communities due to prevailing environmental filtering (communities situated on the blue line or close to it). (B) Decoupled PD-FD patterns: (III) Decoupled phylogenetic diversity (high PD coupled with low to medium FD, or low FD coupled with high to medium PD) may result from trait convergence in distant lineages induced by environmental filtering or habitat tracking of pre-adapted phenotypes due to environmental changes (communities below the blue line); and (IV) Decoupled functional diversity (high FD coupled with low to medium PD, or low PD coupled with high to medium FD) may result from adaptive radiation in closely related species on evolutionary scales or ecological selection over fine spatial and short temporal scales (communities above the blue line). (C) Summary of hypotheses on PD-FD patterns in European grasslands. Env. – environmental.

no universal effect of relatedness on the strength of competition among species. Similarly, the assumption of higher functional similarity among closely related plant species (Fig. 1A, sector II) cannot be taken for granted, since ecological niches and the related functional traits may change over time and evolve convergently within different lineages or rapidly diversify within a set of closely related lineages (Blomberg et al. 2003, Cavender-Bares et al. 2004, Cahill et al. 2008, Cadotte et al. 2017). Thus, the patterns of decoupled diversity in communities may occur either when species are functionally more similar than would be expected from their phylogenetic relationships according to the competitive exclusion – environmental filtering paradigm (decoupled PD, Fig. 1B, sector III; Cavender-Bares et al. 2004), or when they exhibit high trait variation within a limited number of closely related lineages (decoupled FD, Fig. 1B, sector IV; Prinzing et al. 2008, de Bello et al. 2017). On one hand, decoupled PD is characterized by phylogenetic overdispersion caused by environmental filters that select traits important for survival in the specific habitat and are convergent across distant lineages (e.g. Warming 1909, Ackerly 2004, Cavender-Bares et al. 2004, Weiher 2011). On the other hand, decoupled FD is characterized by phylogenetic clustering that occurs when close relatives have filled a range of ecological niches either by in situ adaptive radiation or by dispersal and colonization of conserved ecological types (Gillespie 2004, Prinzing et al. 2008).

Recently, there have been several attempts to disentangle PD and FD facets of different species assemblages and assess the unique information provided by each of these two biodiversity components (Cadotte et al. 2013, 2017, de Bello et al. 2017, Tucker et al. 2018). Still, a knowledge gap remains when it comes to decoupled PD-FD patterns, especially in communities of specific taxonomic groups (such as vascular plants) across broad spatial extents and various environmental and biogeographic contexts. More generally, we are lacking knowledge on how rare or frequent the decoupled patterns are in ecological communities, if they are spatially structured, and what are the underlying community assembly mechanisms. Here, we used plant communities of European grasslands as model ecosystems to evaluate the occurrence of decoupled PD-FD patterns. Grasslands are the second most widespread (semi-)natural ecosystem type after forests in Europe (European Environment Agency 2016). Despite considerable knowledge on their species composition and richness (e.g. Chytrý et al. 2020, Biurrun et al. 2021), evolution and ecosystem function (e.g. Klimešová et al. 2021), our understanding of the relationships between PD and FD in grassland communities is deficient. Such knowledge could elucidate the community-assembly mechanisms and evolutionary history of this ecosystem type.

The contemporary plant species pools of European grasslands largely result from historical biogeographic events such as the Quaternary glacial-interglacial cycles. Related changes in the extent of grasslands through space and time affected the processes of speciation, extinction and exchange of species among different habitats (Pärtel et al. 2005). During the Last Glacial Maximum (LGM), species of dry and alpine grasslands (steppe-tundra) were widespread across Europe (Chytrý et al. 2019), due to the prevailing cold and dry climate. In contrast, species of mesic to wet grasslands were probably restricted to small areas with suitable microclimatic, edaphic and moisture conditions. During interglacials, when mesic conditions prevailed, grassland species were restricted to sites with edaphic or climatic conditions suboptimal for forest growth (Leuschner & Ellenberg 2017b), and larger patches of grasslands existed mainly in the alpine and (forest-)steppe zone (Pärtel et al. 2005). To some extent, open habitats with grassland species were maintained by moderate disturbances, such as wildfires, flooding or grazing by large herbivores, and in the Holocene, by human disturbances (Vera 2000, Svenning 2002, Feurdean et al. 2018). Currently, natural and semi-natural grasslands occur across a wide range of environmental conditions in Europe and harbour a major portion of European plant biodiversity (Squires et al. 2018, Chytrý et al. 2020). This, together with their rich biogeographic history, makes them a good model for exploring the variability of PD-FD relationships.

We used a comprehensive dataset initially consisting of more than 250,000 grassland vegetation plots. These were divided into four broad habitat groups: dry, mesic, wet and alpine grasslands, which represent the main grassland habitat types of Europe (Chytrý et al. 2020). Considering long environmental and geographic gradients these habitat types cover and their complex Quaternary history, we expected differences in the structure of their PD and FD. Besides a common approach to quantifying functional diversity based on a combination of several plant traits (e.g. Westoby & Wright 2006, Díaz et al. 2016), we also evaluated the diversity (variability) of each trait separately because different traits reflect different trade-offs for plant function and affect specifically plant survival. For example, while leaf traits often reflect differences in resource acquisition (Wright et al. 2004), seed mass is important for dispersal and survival in juvenile stages, and plant height and clonality are related to species competitiveness (Díaz et al. 2016).

For each grassland habitat group, we examined differences in the PD-FD relationship, potential underlying factors of these differences, and identified areas that are centres of decoupled phylogenetic and functional diversity in European grasslands.

We expected that the coupled PD-FD pattern prevails in European grasslands, especially in areas with long-term relatively stable environmental conditions. This involves, on the one hand, functionally diverse communities consisting of multiple lineages in benign environments, such as mesic and wet grasslands (Fig. 1A, sector I) and, on the other hand, phylogenetically and functionally clustered communities selected by harsher environments, such as dry grasslands (Fig. 1A, sector II). Nevertheless, in this study, we explicitly focused on the decoupled PD-FD patterns in European grasslands; we expected they occur in communities directly affected by large-scale environmental changes related to Quaternary glacial-interglacial cycles and their interplay with either strong local environmental filters or recolonization processes. In particular, we hypothesized that (i) decoupled phylogenetic diversity (Fig. 1B, sector III) results from high PD linked to persistence of unrelated lineages in refugia, in which they were exposed to pronounced environmental filters for a long time, causing a decrease of FD. This may be the case of some mountainous areas of central and southern Europe where diverse environments could have harboured many different lineages of grassland species in both the glacial and interglacial refugia, and where harsh climate conditions (e.g. cold in alpine environments or drought in steppe environments) have filtered functionally similar species. Further, we hypothesized that (ii) decoupled functional diversity (Fig. 1B, sector IV) is related to low PD reflecting phylogenetically non-random extinctions driven by climate change, and medium to high FD as functionally variable species are selected from the limited pool of available species that may need to occupy distinct niches for coexistence. This may be the case of lowlands of northern and eastern Europe, i.e. non-refugial areas that had been most affected by glaciation or exposed to glacial climates, and where the postglacial recolonization was limited (e.g. Dahl 1998). Our hypotheses are summarized in Fig. 1C.

We assumed the patterns found would differ among grassland habitat groups and individual traits, mirroring their specific biogeographic history and ecology.

Materials and methods

Vegetation data

We obtained 465,629 georeferenced plots (also referred to as 'communities') of grassland vegetation from the European Vegetation Archive (EVA; Chytrý et al. 2016; accessed on 18 September 2019). Our study area was Europe, but the data density for individual grassland habitat groups varied greatly among countries, being highest in the temperate zone (see Supplementary Fig. S1), while northern and eastern parts of the continent were represented by sparse data.

Based on their species composition and cover, we classified all plots of the initial dataset into habitat types according to the European Nature Information System (EUNIS), using the EUNIS-ESy expert system (Chytrý et al. 2020, see also https://floraveg.eu/habitat). We further selected only those plots classified as grassland habitat types and merged the habitats (EUNIS Level 3) into broad habitat groups (approx. EUNIS Level 2), of which we analysed four groups (hereafter referred to as 'habitat groups'): dry, mesic, wet and alpine grasslands. Other groups such as sandy, rocky and saline grasslands were not analysed because of their highly uneven geographical distribution. We removed unclassifiable plots and plots with a cover of trees or shrubs higher than 10% from the dataset, as these could be transitional stages between the habitat groups or non-grassland vegetation, respectively. The number of plots after dataset filtering was n = 285,781.

The filtered dataset was further reduced by including only plots that fulfilled the following three criteria: (i) Sampling date was from 1970 onwards to reduce the effect of long-term vegetation changes. We omitted plots without sampling date. (ii) Location uncertainty of plots was lower than 7 km (keeping plots georeferenced into ~10 km × 10 km grid cells). (iii) Plot size fell within the range of 10–100 m^2, i.e. the sizes traditionally used for sampling grasslands in most of the European phytosociological schools (Westhoff & van der Maarel 1978). These sizes were most common in our dataset. We also kept plots with unknown size (34.5% of the final dataset), since an important part of the geographical coverage (e.g. most of France) would be lost otherwise. As majority of the plots with known sizes fell within the selected range, we assumed that most of the plots with unknown sizes would also fall within that range. We also made a linear model of species richness against plot size on a log-log scale for the plots with known size, separately for each habitat group. The plots with missing size information were then checked by predicting their size using these models. For all of them, the plot size was predicted into the range 10–100 m^2 (results not shown). Number of plots after this filtering step was n = 174,369.

Further, we applied two-step resampling to reduce high density of sampling in some areas and to obtain a more spatially balanced dataset. First, to reduce high sampling densities at fine spatial scales, we followed the approach developed by Divíšek & Chytrý (2018) combining spatial distance between vegetation plots and similarity in species composition. If two plots were closer than 1 km and, at the same time, their compositional similarity measured using the Simpson index was 0.8 or higher, then just one randomly selected plot from the pair was retained (filtered dataset n = 130,842 plots). Second, to reduce differences in plot densities between large regions or countries (e.g. high density in Slovakia vs. low density in Hungary), we performed an additional resampling following Axmanová et al. (2021). We calculated the density of plots belonging to each EUNIS Level 3 grassland habitat type for each country. Subsequently, a threshold defining outlier values of density (upper quartile + 1.5 × interquartile range) was calculated for each habitat type. All combinations of country and habitat type exceeding the respective density threshold were then rarefied, i.e. the number of plots for a particular habitat type per country was decreased to match the threshold level. In this procedure, the plots to be kept (to match the threshold) were selected randomly, but preferring those with a higher proportion of species with available trait data and those with known sizes (filtered dataset n = 95,362).

We considered only angiosperm plant species in the analyses. We excluded plant records determined at the genus or higher taxonomic level, trees, shrubs taller than 0.5 m and woody lianas. This filtering step was performed because these taxa could highly influence the PD or FD of some plots due to their outlying phylogenetic position or trait values. We unified taxonomic nomenclature according to The Plant List (2013), using the R package ‘Taxonstand’ (Cayuela et al. 2017). We merged all the intraspecific taxa to the species level. Plots with less than five species were excluded from the analyses. We used only those plots for which information on a particular trait (see the next section) was available for at least 80% of species. Within these plots, we excluded species with missing trait values (0–20%) from the analyses.

The final dataset comprised 81,484 plots containing 4,119 species: 22,627 plots of dry grasslands (3,343 species), 31,997 of mesic grasslands (2,699), 22,369 of wet grasslands (2,458) and 4,491 of alpine grasslands (1,788). However, the actual number of plots analysed in each habitat group varied among traits, depending on the availability of trait values for at least 80% of species recorded in a plot.

See Supplementary materials for an overview of the final plot numbers from contributing databases (Supplementary Table S1), the information on merging the EUNIS grassland habitat types into broad grassland habitat groups (Supplementary Table S2), and the number of plots used in separate trait-habitat analyses (Supplementary Table S3).

Data on phylogeny, functional traits and the environment

A phylogenetic tree of European grassland species was reconstructed from the supertree of Zanne et al. (2014) as provided by Qian and Jin (2016). Species missing in the phylogeny (40%) were added randomly on one branch within the respective genus using the ‘congeneric.merge’ function in the R package ‘pez’ (Pearse et al. 2015).

Data on five important functional traits suggested by Díaz et al. (2016) were obtained from the TRY database (Kattge et al. 2020; TRY data requests no. 5266 and 5394, see Supplementary Data S1 for citations of individual databases that provided data on the traits used). These traits were plant height, leaf area, specific leaf area, leaf nitrogen content and seed mass. Additionally, we used data on the lateral spreading distance by clonal growth (hereafter ‘lateral spread’) from the CLO-PLA database (Klimešová et al. 2017), as the ability of clonal growth is a very important trait in temperate plant communities, especially grasslands. These traits pertain to fundamental aspects of plant life, such as competition, resource acquisition and reproduction (Díaz et al. 2016). We obtained additional data for plant height using the upper height measurements documented in two published sources on the European flora (Tutin et al. 2005, Tison & De Foucault 2014).

Ecologically relevant environmental variables were obtained from CHELSA v.1.2 (Karger et al. 2017) and ENVIREM v.1.0 (Title & Bemmels 2018), both at a resolution of 30 arc seconds per grid cell. We used 19 bioclimatic variables available in CHELSA in combination with 18 variables and two topographical indices available in ENVIREM (see Supplementary Table S4). Using the R package 'raster' (Hijmans et al. 2020), we extracted mean raster values for the UTM grid cells of 50 km × 50 km in which phylogenetic and functional diversity was mapped (see below).

Phylogenetic and functional diversity

Patterns of decoupled phylogenetic and functional diversity were explored in two ways: (i) separately for each habitat group (dry, mesic, wet and alpine grasslands), where FD was a single combined measure based on five of the six available plant traits (plant height, leaf area, specific leaf area, leaf nitrogen content and seed mass), and (ii) separately for each trait within each habitat group, where FD measures diversity (variability) of a single trait. In this latter case, we obtained 22 trait-habitat combinations, i.e. 5 traits × 4 grassland habitat groups, along with lateral spread available for enough species present in the mesic and wet grasslands only. The lack of data for lateral spread was also the reason for not including this trait into the combined FD measure. The number of plots used for the analyses of particular trait-habitat combinations is in Supplementary Table S3.

We log-transformed the trait values because of their strongly right skewed distributions and square-rooted phylogenetic distances between species (following Letten & Cornwell 2015), considering that evolutionary relatedness is not linearly related to ecological distance between species, thus making phylogenetic and functional distances better comparable.

We calculated PD and FD as mean pairwise distance (MPD) between the species within each plot using the R package 'picante' (Kembel et al. 2010). Given the differences in species richness across the dataset, we calculated standardized effect sizes (SES) of PD and FD. The respective null models (following Gotelli & McCabe 2002) were based on 999 simulations, keeping for each run the number of species in a plot and randomly selecting species from the species pool of the particular habitat group (i.e. dry, mesic, wet or alpine grasslands) to which the plot belonged.

To gain additional insights into the patterns of decoupled diversity at a phylogenetically meaningful taxonomic level, we calculated the relative species richness of vascular plant families (Večeřa et al. 2021). Such a measure helped us to explore which parts of the phylogenetic tree can be responsible for the patterns found, as well as to better understand the mechanisms behind the decoupled diversity patterns from the community-level perspective. Relative species richness was calculated for each plot and each plant family as the number of species belonging to a family divided by the total number of species in a plot. The results for individual plant families were then fitted as vectors onto scatterplots showing the relationship between PD and FD using the 'envfit' function from the R package 'vegan' (Oksanen et al. 2019).

Phylogenetic signal

We tested for phylogenetic signal for each trait by calculating Pagel's λ (Pagel 1999), which is suitable for complex models of trait evolution (Münkemüller et al. 2012). The analysis was done separately within the species pool of each grassland habitat group, i.e. dry, mesic, wet and alpine grasslands.

Degree of decoupling

To identify communities exhibiting decoupled PD or FD patterns, we considered deviations from the positive 1:1 trend line between standardized effect sizes of PD and FD ($SES_{FD} = SES_{PD}$). We used the perpendicular distance of each plot from the 1:1 trend line as a measure of the 'degree of decoupling' (D), assuming the more distant plots to exhibit stronger decoupling (Fig. 2). Patterns of D were visualized using scatterplots and beanplots. The actual relationships between PD and FD measured with SES were quantified with Spearman correlation coefficient.

To compare the tendencies in decoupling towards decoupled PD or decoupled FD, we classified plots into six intervals according to their distance (measured in SES units) from the 1:1 trend line: (a) $D > 0$ and $D < 1$; (b) $D \geq 1$ and $D < 2$; and (c) $D \geq 2$ at the PD side of the trend (below the solid green line in Fig. 2); and (d) $D < 0$ and $D > -1$; (e) $D \leq -1$ and $D > -2$; and (f) $D \leq -2$ at the FD side (above the solid green line in Fig. 2). Subsequently, we used the chi-squared test to assess how proportions of plots within the pairs of intervals mirrored along the 1:1 trend line (e.g. a vs. d) differ from each other, considering the equal distribution as a null expectation. We suggest that distributions markedly shifted from zero (i.e. plots occurring significantly more frequently within all the three intervals on just one side of the 1:1 trend line) indicate a strong tendency towards decoupling. P-values for each habitat group (in the comparison of the combined PD and FD measures) and each trait-habitat combination (in the comparison of individual traits within habitat groups) were adjusted using the Bonferroni correction across the intervals.

Spatial and environmental patterns of decoupling

Given the high local variation in the direction and degree of decoupling at the level of vegetation plots in some areas, we assigned the plots to UTM grid cells of 50 km × 50 km and calculated an average degree of decoupling for each grid cell, separately for each habitat group. Only grid cells with at least 10 plots were considered. These were mapped using the R packages 'raster' (Hijmans et al. 2020), 'rgdal' (Bivand et al. 2020), 'spatialEco' (Evans et al. 2020) and 'berryFunctions' (Boessenkool 2020). We also prepared maps with SES of PD and FD separately for each UTM grid cell. Following Večeřa et al. (2021), we further provide two 'uncertainty maps' for each trait-habitat combination, indicating the confidence of the patterns found for each grid cell: (i) summing up the number of plots, and (ii) showing the standard error of the mean (SEM) of the degree of decoupling.

To evaluate the relationships between the degree of decoupling, environmental variables, and geographical location, we calculated a series of correlations (Spearman correlation coefficient) for each habitat group and each trait-habitat combination based on grid cell values.

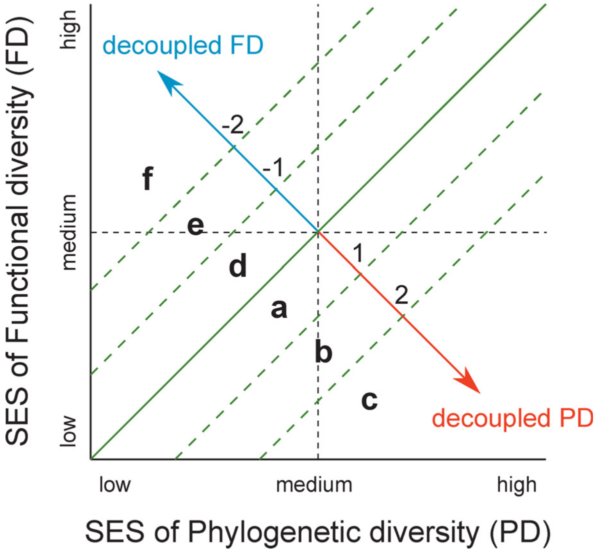


Fig. 2. A scheme of measuring the degree of decoupling. The perpendicular distance from the 1:1 trend line (solid green) expresses the deviation from the expected relationship between standardized effect sizes (SES) of phylogenetic diversity (PD) and functional diversity (FD). The higher the distance, the stronger the decoupling – towards either highly decoupled PD (red, positive distance) or highly decoupled FD (blue, negative distance). Six distance intervals (a–f) are defined according to the distance measured in SES units from the 1:1 trend line.

The data we used were processed and analysed using R version 4.2.1 (R Core Team 2022) and JUICE software (Tichý 2002).

Results

Decoupling in phylogenetic and functional diversity

Correlations between the combined PD and FD measures in each of the four grassland habitat groups were close to zero (rho ~ 0.04–0.19; P < 0.001, Supplementary Fig. S2A). The same applies for individual trait-habitat combinations (rho ~ –0.11–0.22, for P-values see Fig. 3), indicating a weak relationship between phylogenetic and functional diversity in European grasslands. Instead, we found different proportions of communities tending either towards coupled or decoupled PD-FD patterns across different grassland habitat groups and trait-habitat combinations. We also observed greater variability in the PD of communities compared to FD. A marked difference exists between mesic and wet grasslands, which exhibited a wider range of PD (including a ‘tail’ of communities with highly clustered PD and random FD), and dry and alpine grasslands, which exhibited a relatively narrow range of PD (Fig. 3, Supplementary Fig. S2A).

In the combined diversity measure, a large portion of plots in each of the four habitat groups was concentrated close to the 1:1 trend line within the intervals a and d (33–59%), indicating the coupled PD-FD pattern (Fig. S2B). At the same time, a similar number of communities (37–65%) exhibited a degree of decoupling ≥ 1, being located within the

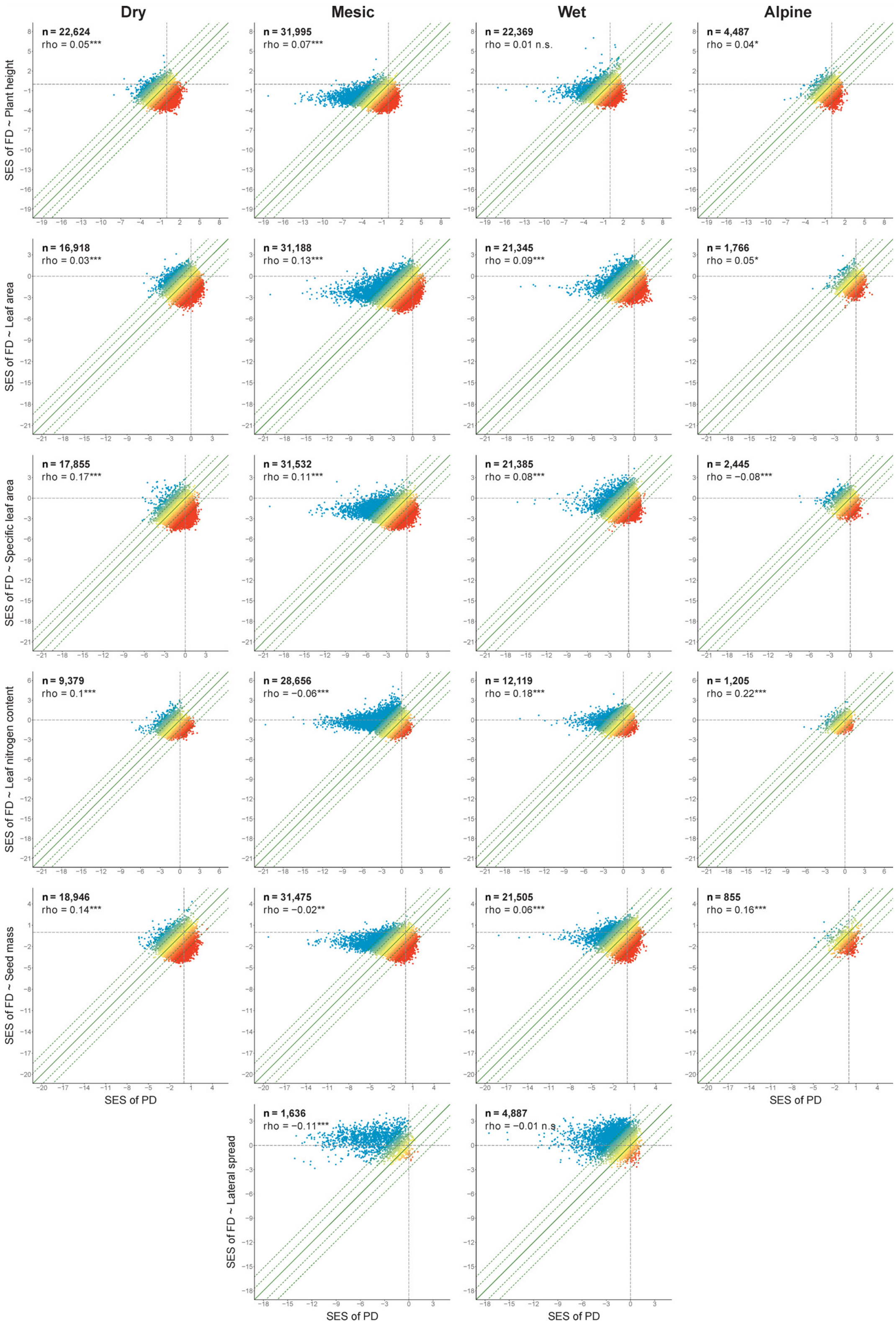

Dry
Mesic
Wet
Alpine
SES of FD ~ Plant height
n = 22,624
rho = 0.05***
n = 31,995
rho = 0.07***
n = 22,369
rho = 0.01 n.s.
n = 4,487
rho = 0.04*
SES of FD ~ Leaf area
n = 16,918
rho = 0.03***
n = 31,188
rho = 0.13***
n = 21,345
rho = 0.09***
n = 1,766
rho = 0.05*
SES of FD ~ Specific leaf area
n = 17,855
rho = 0.17***
n = 31,532
rho = 0.11***
n = 21,385
rho = 0.08***
n = 2,445
rho = −0.08***
SES of FD ~ Leaf nitrogen content
n = 9,379
rho = 0.1***
n = 28,656
rho = −0.06***
n = 12,119
rho = 0.18***
n = 1,205
rho = 0.22***
SES of FD ~ Seed mass
n = 18,946
rho = 0.14***
n = 31,475
rho = −0.02**
n = 21,505
rho = 0.06***
n = 855
rho = 0.16***
SES of PD
SES of PD
SES of FD ~ Lateral spread
n = 1,636
rho = −0.11***
n = 4,887
rho = −0.01 n.s.
SES of PD
SES of PD

Fig. 3. The relationship between standardized effect size (SES) of phylogenetic diversity (PD) and functional diversity (FD) of individual traits separately for grassland habitat groups across Europe. Lateral spread was analysed for mesic and wet grasslands only as the trait values were not available for enough species present in the other habitat groups. n – number of vegetation plots used; rho – Spearman's correlation coefficient and its significance (P-value * ≥ 0.01 and < 0.05; ** ≥ 0.001 and < 0.01; *** < 0.001) are shown. Solid green line – the positive 1:1 trend line between standardized effect sizes of PD and FD; dashed green lines define distance intervals from the 1:1 trend line (see Fig. 2 for details). In the red-blue colour scale with a symmetrical colour intensity along the 1:1 trend, the red colour indicates a higher tendency of plots towards decoupled PD, while the blue colour indicates a higher tendency of plots towards decoupled FD.

intervals b and c on the PD side of the trend line (below the trend line in Fig. 2), which was significantly more than at the opposite side of the trend (see Supplementary Table S5A for the chi-square test results). This shift in the distribution indicates a prevailing tendency towards decoupled PD (i.e. relatively high PD coupled with relatively low FD) in all four habitat groups, most markedly in dry grasslands. By contrast, very few communities (1–6%) exhibited a degree of decoupling ≤ –1, being located within the intervals e and f (above the trend line in Fig. 2), which corresponds to a tendency towards decoupled FD (i.e. relatively high FD coupled with relatively low PD).

In individual trait-habitat combinations, the patterns of (de)coupling were more variable. Most communities (52–85%), in all cases except lateral spread, tended towards a coupled PD-FD pattern (Fig. 4, Supplementary Table S5B). If a community tended towards decoupling, it was decoupled PD in most trait-habitat combinations. There were significantly larger proportions of communities within intervals b and c than within intervals e and f (Fig. 4, Table S5B). This is in line with the results considering the combined diversity measure (Fig. S2B). However, we also found cases of significant overall tendency towards decoupled FD in some trait-habitat combinations.

The most marked tendencies towards decoupled PD were found for dry grasslands in plant height, specific leaf area and seed mass, alpine grasslands in leaf area and seed mass, and wet grasslands in plant height. In contrast, the most marked tendencies towards decoupled FD were found for mesic grasslands in leaf nitrogen content, and mesic and wet grasslands in lateral spread (Fig. 4).

Our additional analyses showed that communities tending towards decoupled PD often contained a remarkably high proportion of orchids. A similar pattern was found for *Cyperaceae*, which often occurred in communities tending towards decoupled PD especially in dry grasslands. In contrast, communities tending towards decoupled FD are predominantly composed of grasses (*Poaceae*), with frequent occurrence of *Urticaceae* (particularly *Urtica dioica*), especially in wet and mesic grasslands. For details, see Supplementary Fig. S3.

Spatial patterns of decoupling

The major patterns in the spatial distribution of the degree of decoupling averaged across individual plots within 50 km × 50 km grid cells were:

(i) In dry grasslands, communities tending towards decoupled PD prevailed in central Europe and partly in the adjacent parts of western Europe (see the combined diversity measure in Supplementary Fig. S4i), whereas communities with coupled PD-FD or

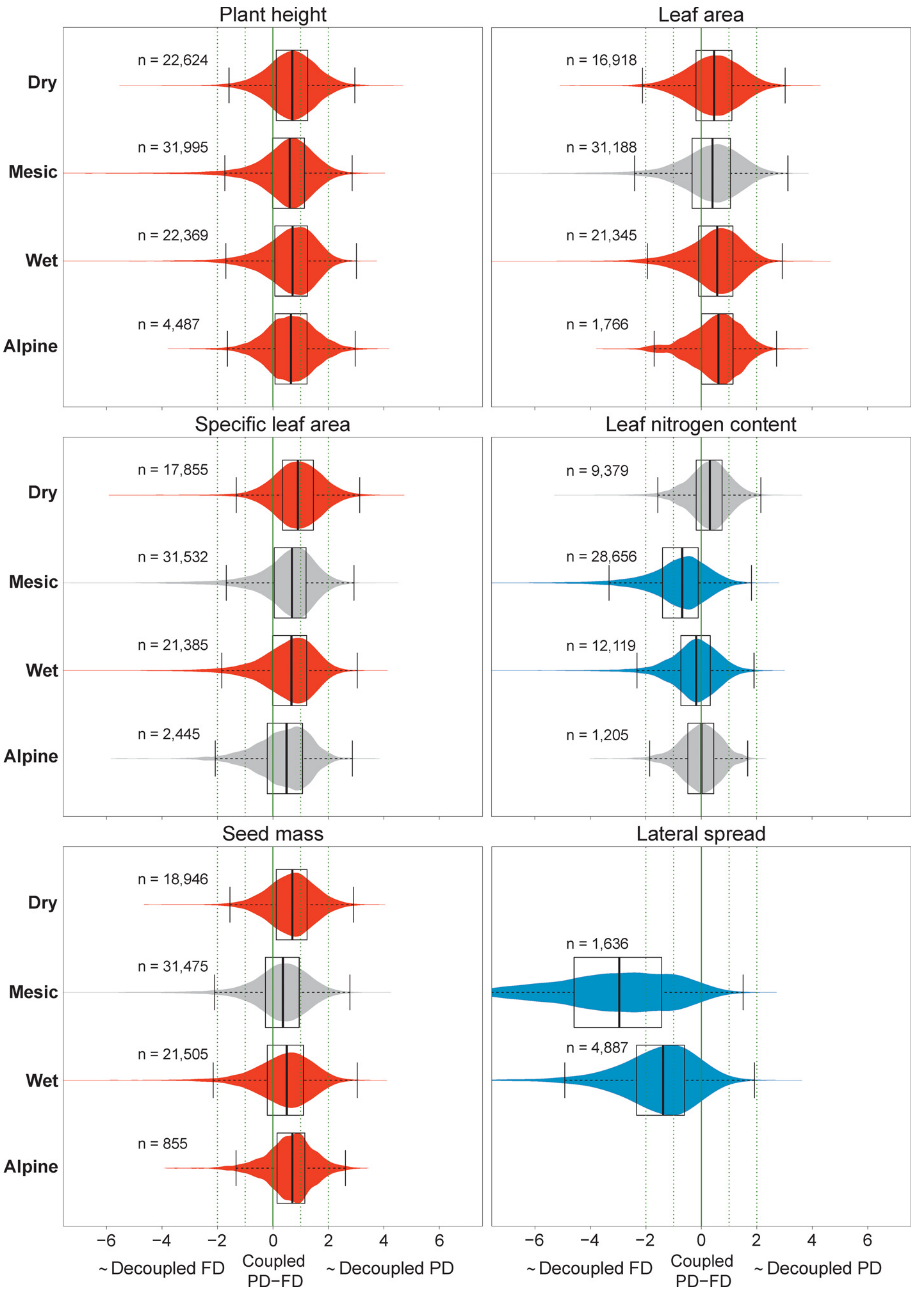


Fig. 4. Degree of decoupling for individual traits in dry, mesic, wet and alpine grasslands across Europe; n – number of vegetation plots used. Solid green line – 1:1 trend between standardized effect size (SES) of PD and FD; dashed green lines – thresholds of three distance intervals in SES units from the 1:1 trend line of coupled PD-FD (see Fig. 2 for details); beans – distribution of distances from the 1:1 trend line; boxplot – median, first and third quartile, minimum and maximum (except outliers); colours of beans: grey – an overall tendency towards coupled PD-FD, red/blue – an overall tendency towards decoupled PD or decoupled FD, respectively, in which plots occur significantly more frequently on one side of the 1:1 trend line (see chi-square test results in Supplementary Table S5).

a slight tendency towards decoupled FD were mostly found in eastern Europe. The latter pattern was detected for individual traits only (Fig. 5A, Fig. S4iiA), namely in plant height, leaf area, specific leaf area, and seed mass (in the two latter traits less distinctively). The patterns of (de)coupling in dry grasslands were mostly driven by differences in PD, which exhibits, on average, a random or slightly overdispersed pattern in central and western Europe and a clustered pattern in eastern Europe. In contrast, FD did not exhibit distinct geographical patterns (except for leaf area), being clustered in most traits throughout Europe (Fig. S4iiA). For leaf area, the more clustered communities were found in central and western Europe.

(ii) In mesic grasslands, communities tending towards decoupled PD were concentrated mostly in (sub)montane areas of central Europe and parts of southern Europe. In contrast, communities tending towards decoupled FD occurred especially in lowland areas of north-western Europe (Fig. 5B, Fig. S4i). This applies to the combined diversity measure as well as all trait-habitat combinations, with the most distinctive patterns found in plant height, leaf area and seed mass (Fig. S4iiB). For leaf nitrogen content, communities tended strongly towards decoupled FD in north-western Europe, while they exhibited mostly coupled patterns in the montane areas. The patterns of decoupling in mesic grasslands were driven by geographical differences in both PD and FD, where PD was strongly clustered in north-western Europe, while FD was strongly clustered in montane areas (Fig. S4iiB).

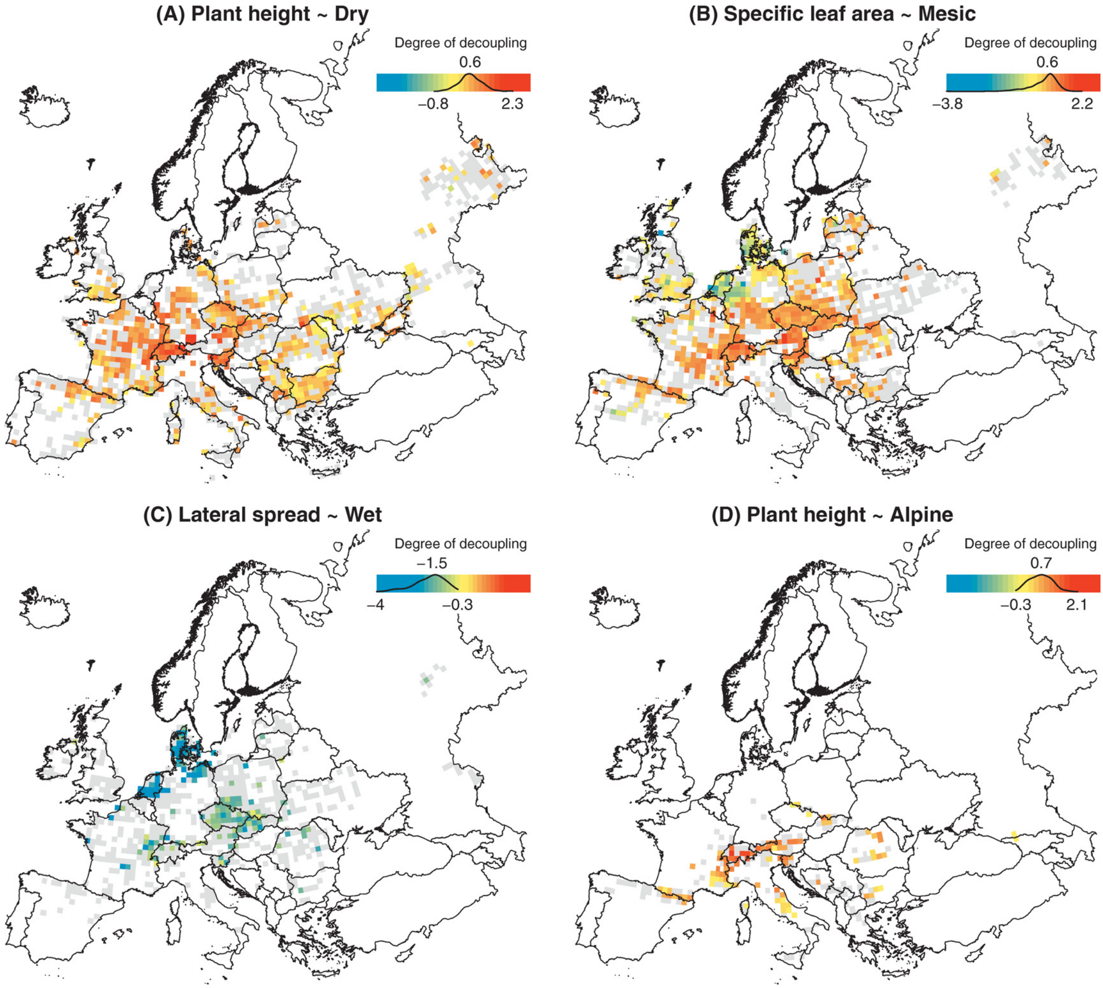
(iii) In wet grasslands, there was no clear geographical pattern in the distribution of the degree of decoupling, except for lateral spread, which differed between north-western Europe (highly decoupled FD) and central Europe (prevalence of coupled PD-FD; Fig. 5C). A similar pattern, though much less distinctive, was visible in leaf nitrogen content. The highly decoupled FD in lateral spread in north-western Europe resulted from low PD coupled with high FD (Fig. S4iiC).

(iv) In alpine grasslands, the tendency towards decoupled PD for plant height, leaf area and specific leaf area prevailed throughout the geographical range of the available data (Fig. 5D, Fig. S4). This was driven, on average, by medium PD and low FD. For leaf nitrogen content, the average degree of decoupling was close to zero, implying a coupled pattern (Fig. S4iiD). For leaf nitrogen content, FD was not as clustered as in other traits in alpine grasslands.

Relationship between the degree of decoupling and the environment

The relationship between the degree of decoupling and environmental variables (both calculated as average values per 50 km × 50 km grid cells) was not strong in most cases (Supplementary Table S6). In dry grasslands, factors related to climatic moisture availability were the most important correlates. The more humid areas harboured communities tending towards decoupled PD, while communities tending towards decoupled FD were more typical of drier areas, as suggested e.g. by the positive correlation between degree of decoupling based on the combined diversity measure (hereafter "-combined") for dry grasslands and climatic moisture index (rho = 0.51). This pattern held in dry grasslands across all the traits studied (Supplementary Table S6).

In mesic grasslands, the most important environmental correlates were related to thermic continentality and topographical heterogeneity. Tendencies towards decoupled PD were connected with more pronounced seasonal changes in temperature and topographically


(A) Plant height ~ Dry

(B) Specific leaf area ~ Mesic

(C) Lateral spread ~ Wet

(D) Plant height ~ Alpine

Fig. 5. Spatial distribution of PD-FD decoupling across Europe in dry, mesic, wet and alpine grasslands for selected traits (A–D) with the most distinct patterns of decoupling. The colour scale (same as in Fig. 3) indicates an average degree of decoupling per UTM 50 km × 50 km grid cells calculated from vegetation plots; the overall tendency is from highly decoupled FD (blue) through the coupled PD-FD (yellow) to highly decoupled PD (red). Grid cells with less than 10 plots are in grey. For each scale, the distribution of the values and the minimum, median and maximum values are shown.

heterogeneous montane areas (e.g. mesic-combined ~ mean diurnal air temperature range: rho = 0.54; ~ terrain roughness index: rho = 0.55), while tendencies towards decoupled FD were typical of flat lowlands under oceanic climate with relatively stable temperatures (e.g. mesic-combined ~ mean daily mean air temperatures of the coldest quarter and of the coldest month: rho = –0.52; Supplementary Table S6). This pattern was consistent in mesic grasslands in all traits except lateral spread. For lateral spread, we found an even more pronounced tendency of decoupled FD towards oceanic climate, both in terms of thermicity (e.g. ~ sum of mean monthly temperatures > 0 °C: rho = –0.79) and moisture (e.g. ~ precipitation of coldest quarter: rho = –0.56). These particular results are, however, affected by the limited coverage, both spatial and taxonomical, of available data on lateral spread.

In wet grasslands, we found differences among individual traits. For plant height and leaf area, there were no correlations higher than 0.4, suggesting a weak link between the degree of decoupling and the environment. In contrast, lateral spread and leaf nitrogen content exhibited similar patterns to those found in mesic grasslands, with tendencies towards decoupled PD being positively related to higher continentality and topographical heterogeneity (e.g. leaf nitrogen content ~ mean diurnal air temperature range: rho = 0.45; ~ terrain roughness index: rho = 0.46), while tendencies towards decoupled FD were related to more stable temperatures throughout the year and flat terrains (e.g. lateral spread ~ mean daily minimum air temperature of the coldest month: rho = –0.58; ~ topographic wetness: rho = –0.58).

In alpine grasslands, we also found differences among individual traits. Tendencies towards decoupled PD were connected with weaker seasonality in terms of temperature and potential evapotranspiration, which applied to leaf area and specific leaf area (e.g. specific leaf area ~ temperature annual range: rho = –0.65), and with higher climatic moisture availability, valid for both leaf area traits and plant height (e.g. plant height ~ climatic moisture index: rho = 0.60). We found weak links to environmental variables for leaf nitrogen content and seed mass in alpine grasslands. There were very limited data, especially for the latter trait.

The collinearity patterns among the variables within individual grassland habitat groups are shown in Supplementary Fig. S5.

Phylogenetic signal in functional traits

Our tests of phylogenetic signal on the level of species pools revealed differences between individual trait-habitat combinations. Across traits, we found the weakest phylogenetic signal for leaf area (except for alpine grasslands) and leaf nitrogen content. We detected the strongest phylogenetic signal for seed mass regardless of habitat group. Across habitat groups, we found large differences in the strength of phylogenetic signal for individual traits, with the lowest mean phylogenetic signal in mesic and alpine grasslands (Supplementary Table S7).

Uncertainty maps

To evaluate the uncertainty of the spatial patterns of the degree of decoupling, we prepared two additional sets of maps. First, we summed up the numbers of plots per 50 km × 50 km grid cells because the patterns of the degree of decoupling might be affected by variable sampling intensity. The average number of plots per grid cell (calculated from grid cells with more than 10 plots) was 39 in dry, 54 in mesic, 40 in wet and 29 in alpine grasslands. The distribution of numbers of plots was uneven and scattered throughout Europe, with higher numbers slightly more frequent in some areas of central and western Europe. The second uncertainty measure was the standard error of the mean (SEM) of the degree of decoupling, capturing the variability in the degree of decoupling among individual communities from which it was averaged for the 50 km × 50 km grid cell. The average SEM of the degree of decoupling was similar across grassland habitat groups. It was 0.16 for dry, 0.18 for mesic, 0.19 for wet and 0.17 for alpine grasslands. The slightly higher SEM for wet grasslands can mirror their relatively higher local variability in the degree of decoupling. The geographical distribution of SEM also showed no distinct patterns (see Supplementary Fig. S6 for the 'uncertainty maps').

Discussion

(De)coupling of phylogenetic and functional diversity

Analysing an extensive set of vegetation plots representing local plant communities, we found that the coupled PD-FD pattern prevails in grassland communities across Europe, which is in line with common expectations (Cadotte et al. 2008, 2019). However, we also detected numerous communities exhibiting a tendency towards the decoupled PD-FD patterns and found differences in degree and direction of decoupling between individual combinations of traits and grassland habitat groups.

The proportion of communities tending towards the coupled or the decoupled patterns found in European grasslands reflects the results of previous studies from other regions or other vegetation types, which mostly found the coupled PD-FD pattern, while a few studies detected decoupled PD-FD patterns, attributed to a combination of different levels of environmental filtering and competition patterns within communities (Cadotte et al. 2017, 2019).

Our results only partly support the general expectation of ecological similarity among closely related species, i.e. niche conservatism (Webb et al. 2002, Kraft et al. 2007). A necessary prerequisite for a coupled PD-FD pattern is a strong phylogenetic signal in traits (Swenson & Enquist 2009, Cadotte et al. 2019). In our study, there are large differences in the strength of the detected phylogenetic signal between the studied traits. The strongest signal we found was associated with seed mass, suggesting that closely related species are more similar in the patterns of seed dispersal and seedling establishment. This is consistent with findings of several previous studies (e.g. Freckleton et al. 2002, Götzenberger et al. 2012, E-Vojtkó et al. 2023). Similarly, strategies related to the competition for light (plant height) and nutrient economy (leaf traits) are phylogenetically conserved within the species pools of grassland habitats, which is in line with previous findings as well (e.g. Prinzing et al. 2001). These results might suggest that the phylogenetic niche conservatism plays an important role in the community assembly process of European grasslands. However, we found both patterns of coupled and decoupled diversity to be quite common, which suggests that the strength of the phylogenetic signal detected on the species-pool level can only partly explain the patterns found on the level of local communities.

In grassland communities across Europe, we identified frequent tendencies to (i) phylogenetic overdispersion connected with functional clustering (decoupled PD), likely induced by a long-term effect of environmental filtering and/or disturbances, especially in dry, alpine and some mesic grasslands; and less often (ii) phylogenetic clustering connected with functional overdispersion (decoupled FD), induced possibly by ecological interactions, especially in some mesic and wet grasslands. These findings of the decoupled diversity agree with the results of Prinzing et al. (2008), who found patterns of decoupled diversity to dominate vascular plant communities in the Netherlands, identifying highly decoupled FD as the prevailing case. Similarly, Pipenbaher et al. (2013) detected patterns of decoupled diversity in different karst grasslands in Slovenia. Our results show that the coexistence of species from various phylogenetic lineages with convergent traits is common in European grasslands. At the same time, they support the idea that the coexistence of closely related species in some types of European grasslands is enabled via trait differentiation (Silvertown et al. 2006, Kraft et al. 2015).

Decoupled diversity in European grasslands: ecological and spatial patterns

We found that most grassland plant communities exhibiting the decoupled PD-FD pattern tended towards decoupled PD (i.e. relatively high PD coupled with relatively low FD). Exceptions from this pattern were found for lateral spread in mesic and wet grasslands, and for leaf nitrogen content in mesic grasslands, which showed a strong tendency towards decoupled FD (i.e. relatively high FD coupled with relatively low PD). The prevailing functional similarity among species in grassland communities typical of decoupled PD is likely maintained by (i) long-lasting regular disturbances, e.g. grazing by large herbivores, wildfires, flooding or haymaking; and (ii) relatively extreme environmental conditions in naturally treeless areas, especially stress from cold, drought and wind-induced desiccation in alpine and dry grasslands (Poschlod et al. 2009, Purschke et al. 2013, Leuschner & Ellenberg 2017b). These ecological factors allow only certain trait combinations to occur (i.e. relatively low FD). However, these combinations can occur in many different plant lineages. In particular, they may affect plant height and leaf traits, for which we found the most marked tendencies towards decoupled PD.

Another component of decoupled PD – the medium to high PD, which is also typical of many grassland communities – generally results from a higher relative representation of different clades of forbs at the expense of graminoids. This possibly depends on grassland management or biogeographic history (Večeřa et al. 2021). By contrast, the decoupled FD pattern found in lateral spread and leaf nitrogen content occurs in grasslands dominated by graminoid species with varying capacities of clonal propagation (Klimešová et al. 2021), accompanied by few other species, usually strong competitors with large leaves containing high amounts of nitrogen.

The geographical distribution of decoupling in European grasslands and its environmental correlates seem to be largely affected by the Quaternary history, especially the putative location of glacial and interglacial refugia of grassland species (e.g. Birks & Willis 2008, Divíšek et al. 2022), and also by ecological differences among individual habitats.

Dry grasslands

In dry grasslands, there is a contrast between central Europe and parts of western Europe with communities tending, on average, towards decoupled PD, and eastern Europe, harbouring mostly communities that exhibit the coupled pattern or tend towards decoupled FD. Such a pattern might be explained by several factors.

Compared with eastern Europe, central and western Europe experienced more pronounced climatic changes during the Quaternary, with subsequent habitat shifts ranging from full-glacial steppe-tundra mosaic (Chytrý et al. 2019) to interglacial deciduous broadleaved forests (Leuschner & Ellenberg 2017a). The central-European landscape also has, in general, higher topographical and climatic heterogeneity (Rivas-Martínez et al. 2004) than eastern Europe, providing more sites with mesic conditions. These features likely enabled the survival of ecologically different groups of species during glacial-interglacial cycles and favoured both historical and current exchange of species among habitats, thus likely enlarging the species pool and PD of dry grasslands. The relatively more humid conditions are known to support higher species richness in dry grasslands (Palpurina et al. 2017), which fits our findings that communities tending towards decoupled PD are especially those of semi-dry grasslands, occurring at less dry sites and containing both xerophilous and mesophilous species.

The other component of decoupled PD in dry grasslands across central and western Europe – medium to low FD suggests the effect of environmental filtering (Pausas & Verdú 2010), which may be attributed to sites with extreme soil pH (both low and high) and/or relatively shallow and infertile soils (see Pipenbaher et al. 2013). The effects of these factors could have been further strengthened or complemented by regular medium-intensity management that contributed to forming the diversity of semi-natural grasslands over centuries or even millennia (Poschlod et al. 2009, Janišová et al. 2021). However, no data on the grassland management history are available for the pan-European extent.

In contrast, the lowland steppe areas of eastern Europe have been environmentally more stable, with relatively harsh climates determining the occurrence of (forest-)steppe(-tundra) habitats during both glacial and interglacial periods (Simakova 2006, Allen et al. 2010). An absence of refugia in topographically uniform landscapes coupled with dry continental climate resulted in overall lower PD of dry grasslands in eastern Europe than in central and western Europe. However, dry grasslands in eastern Europe are not functionally clustered in general. In some traits, such as plant height, they exhibit a random pattern, suggesting that the prevailing dry conditions have not selected functionally uniform communities in all cases.

As an example how the patterns of decoupled diversity at the community level can be ‘translated’ into the meaningful taxonomic perspective, we calculated for each community the proportion of species of individual plant families (i.e. relative species richness per family; Večeřa et al. 2021) and checked tendencies of individual families in relation to the PD-FD relationships. In dry grasslands, we found high relative richness of *Orchidaceae* or *Cyperaceae* to be relatively frequent in communities tending towards decoupled PD. Orchids are known to be particularly frequent in regularly mown or extensively grazed semi-dry grasslands on base-rich soils with low cover and height of the herb layer (Kull 2002, Landi et al. 2009, Slaviero et al. 2016). These communities are among the globally most species-rich at fine scales (Wilson et al. 2012, Chytrý et al. 2015) and are assembled from large species pools containing many forbs and relatively few grasses (Sádlo et al. 2007). In some communities, the high relative richness of *Orchidaceae* and *Cyperaceae* species may balance the overall proportion of monocots vs. eudicots, thus increasing PD.

Mesic grasslands

In mesic grasslands, we also found contrasting geographical patterns that could be attributed partly to Quaternary history and partly to human influence. Communities of mesic grasslands in central and southern Europe tend, on average, towards decoupled PD, whereas those in north-western Europe tend towards decoupled FD. The glacial refugia of mesic grassland species might have been mainly temperate open-canopy forests in southern and central European mountains, forest-steppe mosaics in southern Europe, and meadow-steppe patches at mid-latitudes (Magyari et al. 2014, Janská et al. 2017, Divíšek et al. 2020). Hence, we suggest that the mountains of southern and central Europe have acted as a ‘museum’ (sensu Stebbins 1974), preserving more grassland plant lineages due to their refugial capacity. Species of mesic grasslands made use of relatively more humid conditions in the mountains due to orographical precipitation during glacial periods (e.g. Keppel et al. 2012). At the same time, harsh montane environments (especially effects of cold and wind) likely selected for more functionally clustered communities, which is best detectable in plant height and specific leaf area. The higher PD and lower FD in these mountainous and hilly regions can also be explained by the fact that the southern and central-European grasslands have long been managed regularly, but less intensively, than those in north-western Europe (Sutcliffe et al. 2015, Török et al. 2018, Boch et al. 2020).

Similar to dry grasslands, some mesic grassland communities exhibiting decoupled PD are characterized by the high relative richness of orchids, but also other forbs such as species from *Campanulaceae*, *Polygalaceae* or *Rosaceae*. Such communities are often species-rich mountain hay meadows. For *Campanulaceae*, for example, it has been shown that several species growing in open habitats (including mesic grasslands) tend to converge towards similar plant height and anatomical stem structure, which seems to be primarily related to habitat adaptation (Schweingruber et al. 2014).

Decoupled FD in mesic grasslands can be found mostly in previously glaciated lowlands of north-western Europe. The subsequent recolonization of these areas was performed by a limited number of lineages which, however, might have been able to occupy various niches and assemble into functionally relatively diverse communities (medium to high values of FD). Our results agree with the findings of Prinzing et al. (2008), who concluded that decoupled FD in Dutch plant communities may result from recent ecological interactions (mostly competition) leading to mutual exclusion of closely related species in communities, and their replacement by less similar species from the limited species pool available, often from the same lineage (see also Pausas & Verdú 2010, Gerhold et al. 2015).

Some of the studied grasslands tending towards decoupled FD were characterized by high relative richness of grasses and *Urticaceae* (*Urtica dioica* in particular), which indicates nutrient-rich communities. The markedly low relative richness of other clades of forbs in these species-poor grasslands, especially in north-western Europe (Večeřa et al. 2021), may be likely attributed to the intensive agricultural use of lowland grasslands in this area throughout the modern era (e.g. Silvertown et al. 2006, Bos et al. 2013). Fertilization, coupled with high atmospheric nitrogen depositions (e.g. Duprè et al. 2010), has led to marked eutrophication and subsequent dominance of strong competitors. This has resulted in the impoverishment of grassland communities, characterized by a pronounced clustering of PD. An alternative or complementary factor is the time lag due to post-glacial recolonization of these areas, also potentially resulting in grassland communities with species from relatively fewer families compared with hilly areas of southern and central Europe. This explanation is supported by the fact that the high proportion of grasses at the expense of forbs in north-western Europe is also typical of other habitats, e.g. forests and scrub (Večeřa et al. 2021).

Decoupled FD found in lateral spread in mesic and wet grasslands is a result of high variation in the branching system structure of grasses (Perreta et al. 2011). The variability of lateral spread forms determines several ways grasses explore and utilize resources, including their interactions with neighbouring plants (Grime et al. 1986). The pattern we found is, however, based on data from central and north-western Europe only.

Wet grasslands

In wet grasslands, we did not find any distinct geographical pattern or strong correlation with available environmental variables except those for lateral spread. Wet grasslands occupy patches of suitable environment in terrain depressions and close to streams, regardless of macroclimate. Thus, the degree of decoupling in wet grasslands is likely not so much influenced by historical biogeographic and large-scale environmental factors. It may rather depend on local nutrient availability and disturbance regime, including management practices. The high relative richness of *Orchidaceae*, *Cyperaceae*, and other families of flowering plants such as *Ranunculaceae* or *Rosaceae* in some wet grasslands tending towards decoupled PD is typical of species-rich communities, with low nutrient inputs and possibly long-lasting extensive management. In contrast, wet grasslands tending towards decoupled FD are species-poor communities, often with a high relative richness of *Poaceae* or *Apiaceae*. They can be characterized by nutrient-rich soils, relatively low disturbance levels or intensive management practices, and species composition mainly influenced by biotic interactions, such as asymmetrical competition (e.g. Gerhold et al. 2015). This suggests that the ecological differentiation within wet grasslands is reflected in the features of PD and FD at the community level.

Alpine grasslands

Alpine grasslands adapted to cold climate have survived the interglacial periods, including the Holocene, in isolated areas above the alpine timberline. We found the species composition of these communities to be determined by a prevailing tendency towards decoupled PD for plant height, leaf area and seed mass. Similar patterns were found by Dainese et al. (2015) in the Italian Alps. Decoupled PD of these grasslands may be jointly related to two important features of alpine habitats: (i) The harsh environmental conditions, especially stress from cold and wind, have caused a low FD in plant height and leaf traits; and (ii) the diverse topography, topoclimatic heterogeneity that can buffer macroclimate, and habitat isolation (Sandel et al. 2011) have enabled the persistence and diversification of many lineages leading to relatively high PD (Crisp et al. 2009). The negative correlation between decoupling towards PD and variables related to climatic continentality may reflect the decreasing number of lineages that can tolerate extremely harsh conditions in the frame of the high-elevation environment. The high relative richness of *Cyperaceae*, *Orchidaceae* or *Ranunculaceae* in some alpine grasslands tending towards decoupled PD indicates similar underlying processes as suggested for the other grassland habitat groups. Our results confirm that adaptations to alpine environments have repeatedly evolved in different phylogenetic lineages (Le Bagousse-Pinguet et al. 2018).

Methodological issues

There are several methodological issues and potential limitations of the data and analyses used that can affect the interpretation of our results. To check the phylogenetic-functional relationships, we used a limited set of traits and considered functional diversity not only as a single measure combining these traits, but also as the variability in individual traits. The functional importance of different traits may vary across habitats (Prinzing et al. 2001). For example, traits responsible for resource acquisition may be limiting in stressful environments, while competitive traits may play an important role in productive environments. Thus, we assumed that analysing the diversity of each trait separately could help disentangle the complex relationships between PD and FD. Other traits (e.g. those related to rooting system, allelopathy, phenology, pollination mode or dispersal syndrome) may shape community assembly as well (Klimešová et al. 2008, Lamb & Cahill 2008). These traits would probably differ in their variability and strength of phylogenetic signal (Blomberg et al. 2003). However, data on such traits are missing for many species, especially those with relatively restricted geographical ranges. The traits we used are those most important for species coexistence and competitive abilities (Díaz et al. 2016). Even for the traits analysed, there are certain data gaps. Therefore, we had to exclude some species (mostly rare ones) from vegetation plots for which the trait data were missing and keep only plots with sufficient information on functional trait diversity (at least for 80% of present species). In some cases, this resulted in a strong geographical filtering of the available data. For example, the decoupled FD found in lateral spread and partly leaf nitrogen content is based on data from central and north-western Europe only. Thus, better trait data coverage is needed to confirm some of the patterns found for the pan-European extent.

We also acknowledge that there are several possible ways how PD and FD of plant communities and their theoretical relationship can be estimated. Here, we used MPD as it is not linearly related to species richness (Tucker et al. 2017) and is commonly used for calculating both functional and phylogenetic diversity in similar studies, which makes our results easily comparable with other studies. Further, not all the plots in our dataset have information on species cover/abundance, so we cannot use indices based on this information. To downscale the effect of basal lineages of the phylogenetic tree, we square-root transformed phylogenetic distances between species. Thus, we tried to account for differences in both finer and deeper phylogenetic structure within communities (Letten & Cornwell 2015) and do not expect that the use of other indices would change our conclusions. While accounting for presumed non-linearities between evolutionary relatedness and ecological dissimilarity among species, we adhered to the expectation of a simplified positive linear relationship between PD and FD, according to the ‘competitive exclusion – environmental filtering paradigm’ (e.g. Cadotte et al. 2008, Kelly et al. 2014). We acknowledge that there is a range of alternative evolutionary models (Cadotte et al. 2017), such as the Brownian motion model (Harvey & Pagel 1991), Ornstein-Uhlenbeck model (Hansen 1997, Butler & King 2004) or other complex models incorporating e.g. species interactions. These models can be considered in future studies to find a theoretical relationship between PD and FD which would better align with the case of European grasslands. Still, it is not clear how one single rescaling of phylogeny would be able to accommodate different traits evolving under different models of evolution (Cadotte et al. 2017).

We also acknowledge there are many null-model variants that can be used to obtain standardized effect sizes of PD and FD. The way how species pool is defined, in particular, can significantly affect the outcomes (Cadotte & Davies 2016). We applied a randomization scheme over the whole geographical gradient studied, to account for the expected biogeographic differences in the patterns of PD-FD relationships. At the same time, this was a rather conservative scheme, restricting the pool of species available for randomly sampled communities to those occurring in the respective target habitat (dry, mesic, wet or alpine grasslands), i.e. a habitat-specific species pool.

To avoid high local variation in the degree of decoupling, we calculated an average decoupling and linked it to average values of environmental variables, both within grid cells of 50 km × 50 km. This allowed us to effectively examine the relationship between decoupling and the environment on a pan-European scale, as opposed to using values derived from individual vegetation plots. However, this grid-cell approach might blur the detected relationship in some areas due to high local variation in certain environmental conditions, such as topography in alpine grasslands. Nevertheless, we believe that such cases were not common. The weaker link we observed between decoupling and the environment in some grassland habitat groups (e.g. wet grasslands) or trait-habitat combinations (e.g. seed mass in alpine grasslands) could rather be explained by the omission of local factors, on which data are missing on a pan-European scale, like nutrient availability or microclimate, and lack of trait data, respectively.

Despite the above-mentioned methodological issues and limitations, we believe that our results are valid and point to the important aspect of relationships between PD and FD in European grasslands.

Conclusions

Our study based on a large European grassland dataset shows that phylogenetic diversity (PD) and functional diversity (FD) of vascular plant communities are often not coupled (i.e. not positively correlated). We demonstrate that both decoupled PD and decoupled FD patterns frequently occur in plant communities. Our findings suggest that the communities tending towards decoupled PD and FD occur mainly in areas and conditions historically affected by glacial-interglacial environmental changes. These communities are characterized by processes such as trait adaptations, dispersal and occupation of various ecological niches, which translate into community assembly. This is in contrast with the communities exhibiting the coupled PD-FD pattern that are more likely to occur in long-term stable environmental conditions. We also suggest that these effects are largely specific to certain habitats and certain functional traits. Phylogenetic overdispersion connected with trait convergence (decoupled PD) was the most frequent pattern of decoupled diversity in European grasslands. We suggest that it relates to biogeographic and ecological processes such as species accumulation in Quaternary refugia, convergent evolution of species traits under strong environmental filters, and historical and current grassland management by humans.

The various facets of decoupled diversity patterns have been little explored so far. We believe that patterns of decoupled diversity should receive more systematic scientific attention, considering also ecosystems other than grasslands. Our study suggests potential ways to broaden our understanding of the role of historical and ecological factors in community assembly.

Supplementary material

Data S1. TRY database dataset references.
Fig. S1. Maps of the distribution of individual habitat groups.
Fig. S2. Relationship between PD and FD for the combined diversity measure.
Fig. S3. Relationship between PD and FD and relative species richness of vascular plant families.
Fig. S4. Spatial distribution of the degree of decoupling, PD and FD.
Fig. S5. Collinearity patterns of the considered environmental variables.
Fig. S6. Uncertainty maps.
Table S1. Overview of contributing vegetation-plot databases.
Table S2. Assignment of EUNIS habitat types to broad habitat groups.
Table S3. Numbers of plots used for analyses within trait-habitat combinations.
Table S4. Variables used to examine correlations with the degree of decoupling.
Table S5. Chi-square test results.
Table S6. Correlations of environmental variables and the degree of decoupling.
Table S7. Phylogenetic signal in plant traits.

Supplementary materials are available at www.preslia.cz

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Vztah mezi fylogenetickou a funkční diverzitou evropských travinných společenstev

Studium vztahů mezi fylogenetickou (PD) a funkční diverzitou (FD) je důležité pro pochopení mechanismů formování rostlinných společenstev. Tradičně se předpokládá, že tyto dvě míry diverzity jsou vzájemně korelované a hlavními mechanismy, které určují fylogenetickou a funkční strukturu společenstev, jsou kompetiční vyloučení a filtrace podmínkami prostředí. Řada dílčích studií nicméně nasvědčuje tomu, že tento pohled je neúplný. Některá společenstva se od předpokladu vzájemně korelovaných měr PD a FD odchylují a jsou buď fylogeneticky nadprůměrně rozrůzněná při současné konvergenci funkčních vlastností rostlin (vyznačují se tzv. oddělenou fylogenetickou diverzitou), nebo jsou naopak fylogeneticky relativně homogenní a funkčně nadprůměrně rozrůzněná (oddělená funkční diverzita). V této studii jsme se zabývali vztahem PD a FD ve společenstvech cévnatých rostlin evropské travinné vegetace. Předpokládali jsme, že PD bude ve většině trávníků korelovat s FD a že tento případ bude vázán na dlouhodobě relativně stabilní prostředí. Nekorelovanou PD a FD jsme naproti tomu očekávali v trávnících těch oblastí, které byly nebo stále jsou ovlivňovány dynamickými změnami prostředí, hlavně jejich kvartérní historií. Analyzovali jsme 81484 fytocenologických snímků suchých, mezických, vlhkých a alpinských trávníků, v nichž bylo celkem zaznamenáno 4119 druhů krytosemenných rostlin, a data o šesti jejich funkčních vlastnostech – výšce rostliny, listové ploše, specifické listové ploše, obsahu listového dusíku, hmotnosti semene a vzdálenosti klonálního šíření. Funkční diverzitu jsme hodnotili dvěma způsoby – jednak jako míru založenou na kombinaci pěti ze šesti uvažovaných druhových vlastností, jednak jako variabilitu v každé vlastnosti zvlášť. Druhou variantu jsme zvolili proto, že různé vlastnosti jsou relevantní pro různé funkce rostlin a různé typy trávníků. Zjistili jsme, že vztahy mezi PD a FD jsou v trávnících různorodé v závislosti na typu biotopu, uvažované funkční vlastnosti a geografické oblasti. Korelovaná fylogenetická a funkční diverzita převládala. Nicméně u mnoha společenstev jsme zaznamenali oddělenou PD, která je pravděpodobně výsledkem fylogeneticky diverzifikovaného druhového zásobníku, u něhož byly podmínkami prostředí filtrovány vzájemně podobné vlastnosti druhů. To byl případ zejména suchých trávníků a také většiny dalších typů travinné vegetace, pokud jsme uvažovali výšku rostliny, listovou plochu nebo hmotnost semen. Naproti tomu tendenci k oddělené FD jsme zaznamenali pouze u mezických a vlhkých trávníků v případě obsahu listového dusíku a vzdálenosti klonálního šíření rostlin. Domníváme se, že je to způsobeno mezidruhovou konkurencí a pravděpodobně také historií využití krajiny v daných oblastech. Oddělená fylogenetická diverzita je tedy v evropských trávnících jednoznačně častější, a to zejména v oblastech s členitějším reliéfem ve střední a jižní Evropě a také v částech západní Evropy s mírným klimatem. Tato skutečnost může být způsobena přítomností glaciálních i interglaciálních refugií, která přispěla k zachování mnoha fylogenetických linií. Druhy z těchto linií jsou si však funkčně vzájemně podobné vlivem filtrace specifickými podmínkami prostředí (například stres ze sucha nebo chladu). Naše výsledky potvrzují, že fylogenetická a funkční diverzita mohou odrážet různé aspekty struktury společenstev a mechanismů, které se podílejí na jejich utváření. Domníváme se, že případy oddělené fylogenetické a funkční diverzity ve společenstvech různých organismů jsou stále málo prozkoumány a zasluhují si systematický výzkum.

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