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## Research Article

### The proper middle class: assessing the importance of subordinate species on plant community assembly and functional diversity

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The local species abundance distribution (SAD) and the associated distributions of species functional traits (TADs) both result from the process of plant community assembly. Community assembly has been extensively studied for dominant and rare plants, while subordinates, the species of intermediate abundance in a community, have received less research attention although this group is comparatively species rich and important for community functioning. Here, we study the functional role of subordinate species (those covering the intermediate 50% of abundance ranks) using a large data set of Paeleartic dry and semi-dry grassland plant communities and data on specific leaf area, seed mass and plant height. Our findings indicate that species rank orders of SADs and TADs tend to be negatively correlated, causing the TAD to have higher evenness than the associated SAD. Subordinate species represented on average less than 15% of total plant abundance and trait space. Functional diversity of subordinates was lower than expected by a null model that assumed an equiprobable random

distribution of trait values among plant species. Climate seasonality and elevation appeared to be the most important drivers of subordinate abundance and functional diversity. We conclude that subordinates differ from dominants in trait composition, leading to their partial functional independence from dominants.

Keywords: dominance orders, Palearctic grasslands, plant functional traits, species abundance distribution

## Introduction

Two basic patterns can be used to describe local plant community assembly and functioning: the species abundance distribution (SAD) and the abundance distribution of species functional traits (i.e. the trait abundance distribution, TAD; Koffel et al. 2022), the latter being obtained from the product of species trait values and relative abundances. SADs combine information on species richness and abundances, characterise the patterns of commonness and rarity in the community, and contain information about competitive interactions (Kunin and Gaston 1998, McGill et al. 2007, Matthews and Whittaker 2014). The TAD provides insight into niche occupancy and environmental filtering (Violle and Jiang 2009, Laughlin et al. 2015). Together, these patterns define functional diversity and community functioning (Diaz and Cabido 2001), and influence community stability and dynamics (de Mazancourt et al. 2013).

Concerning the SADs of plant communities, much work has been devoted to the importance of the dominant species for community functioning, particularly productivity, biomass, and carbon sequestration (Grime 1998, Hillebrand et al. 2008, Brun et al. 2022, Engel et al. 2023). The experimental removal of dominant species frequently causes a higher diversity and evenness of plant communities (Souza et al. 2011, Avolio et al. 2019). Dominants have also been shown to control invasibility, and consequently compositional stability (Meiners et al. 2002, Sasaki and Lauenroth 2011). Importantly, Wilfahrt et al. (2023) reported that dominant grassland species in particular decline under rapid environmental change.

Much research in plant community ecology has also focused on the roles of rare species. For example, rare species have been shown to have increased local extinction probabilities but also to often be efficient colonisers (Crisfield et al. 2024). Experimental studies of grasslands have shown that the removal of rare species reduces functional diversity, increasing the susceptibility of communities to invasion by alien species (Lyons and Schwartz 2001). Importantly, the trait space of rare plant species has been found to be relatively heterogeneous, leading to a contribution (in terms of the number of individuals) of this group to the overall functional hyperspace of plant communities that is disproportionate to their abundance (Jain et al. 2014, Leitão et al. 2016). Rare species also contribute to the temporal variability in community composition (Grime 1998). This duality between dominant and rare species has its spatial counterpart at the metacommunity level (Gibson et al. 1999), where the core-satellite concept focuses

on species being regionally common (core species) and those occurring at only a few sites (satellites) (Hanski 1982). Both groups are frequently found to be relatively species rich, leading to a bimodal shape of the species occupancy distribution (Gibson et al. 1999).

As the above discussion attests, a large amount of research in plant community ecology has focused on dominant and rare species. In contrast, surprisingly little work has focused on species with intermediate abundance; that is, those species located between abundant and rare species, or, in terms of occupancy, those species with intermediate regional occurrence, located between core and satellite species (Grime 1998, Bakker and Olf 2003). This group is often imprecisely called ‘subdominant’ although it also encompasses, by definition, species with comparatively low abundance. Here we follow Grime (1998), who classified the group as ‘subordinates’. Subordinates often account for the majority of species in a community, although there is no strict definition of ‘subordinate’, as is also the case for ‘abundant’ and ‘rare’ (Kunin and Gaston 1998, Flather and Sieg 2007, Crisfield et al. 2024). The variability in observed SADs and the intrinsic dependence of SAD properties on the sampling scale make it challenging to apply any ecologically meaningful definition, for instance based on the fraction of total abundance in the case of dominant, or the numbers of singletons in the case of rare species (Enquist et al. 2019). Here, we define these groups from the quartiles of the associated species log abundance-rank order distributions and refer to the middle ranking 50% of species as being subordinate. This definition has the benefit of being operational irrespective of the shape of the underlying SAD (Fig. 1). Thus, this definition allows for direct comparisons between communities and also implicitly defines the meaning of ‘dominant’ (top ranking 25% of species) and ‘rare’ (the bottom ranked 25% of species) and enables us to directly study and compare the effects of subordinates on the variability of dominance hierarchies in communities without the need to account for richness effects and different types of SAD distributions (Avolio et al. 2019).

Ecosystem functioning, quantified by aggregate functions like productivity, carbon sequestration, or ecosystem services, and also the temporal stability and resistance of these functions, is frequently reported to be positively associated with species (Creed et al. 2009, Jochum et al. 2020) and functional diversity (Cadotte et al. 2011). The aggregate functions related to plant growth are assumed to be mainly determined by the abundant species (Avolio et al. 2019) as these frequently make up the largest part of plant cover. However, there is increasing evidence that subordinates play

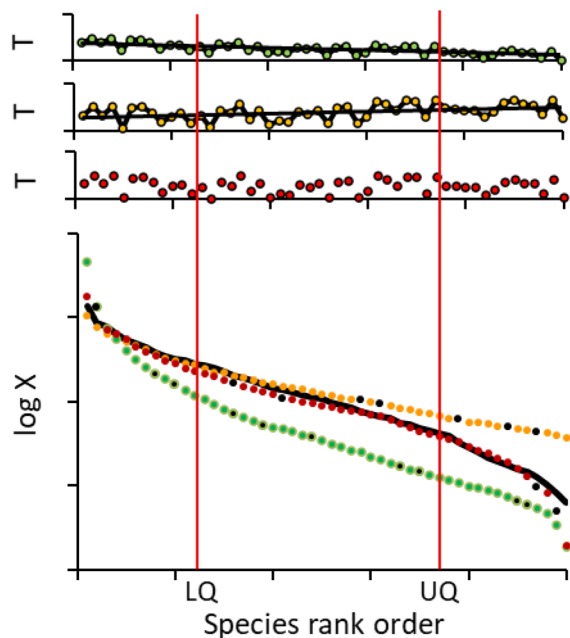


Figure 1. Illustration of possible distributions of trait values along the abundance rank order (top three plots). The bottom plots show the species abundance distribution (SAD, black line) and resulting species trait abundance distributions (TAD, coloured dots), both given in the form of species rank order plots. The latter differ in shape depending on the correlation between species trait values ( $T$ ) and species abundances ( $N$ ), with the product of the two values giving the trait abundance ( $X = N \times T$ ). A random distribution of trait values among species (red dots) retains the SAD shape but leads to an excess of species with low total trait abundance. Positive (yellow dots) or negative (green) rank order–trait value correlations (equivalent to negative [yellow] and positive [green] abundance–trait value correlations) cause TAD distributions to be either less or more even than the SAD distribution. Vertical red lines separate the dominant (lower quartile of species, LQ), subordinate and rare (upper quartile, UQ) species groups according to the SAD. Black dots on each TAD denote species that changed their respective group membership between the SAD and the TAD.

an important role in the maintenance of community stability and resistance. Again, studies that assess the role of subordinates for ecosystem functioning are scarce. Grime (1998) envisaged the role of subordinates as filters for the recovery of dominant species after disturbance. According to this view, subordinates would at least partially control the species composition of dominants in plant communities. Recalling the insurance hypothesis of ecosystem functioning, several studies have hypothesised that subordinates might ensure community functioning after the removal of dominant species, leading to increased community stability (Yachi and Loreau 1999, Sasaki and Lauenroth 2011, Soliveres et al. 2015). However, arguably this would only be possible if the trait space of dominant and subordinate species largely overlaps, a pattern that has rarely been tested empirically. By extension, different trait spaces of dominant and subordinate species should result in pronounced changes in community functioning following disturbance. There have been few tests of

this idea but Mariotte et al. (2013) found that subordinate plant species might stabilise grassland community functioning against drought, and Zelikova et al. (2014) reported that the decline of dominant grassland plant species in a  $\text{CO}_2$  elevation experiment was associated with a more even community structure and increased temporal stability in plant production.

Species abundance (SAD) and species trait abundance (TAD) distributions predictably differ in shape and evenness under local competition and abiotic filter regimes (Fig. 1). Here, we use the term trait abundance to refer to the product of species single trait values and species abundance (i.e. a separate TAD is generated for each individual trait). The concept is therefore closely related to the community weighted mean trait concept introduced by Garnier et al. (2004), but is arguably more informative as it contains information on the full distribution of trait values. The difference between SADs and TADs might also be accompanied by a reordering of species positions along the axis of trait values in comparison to the SAD ordering, possibly causing compositional changes in the dominant, subordinate, and rare species groups (Fig. 1). Because TADs are calculated as the product of trait value and abundance, in a neutral situation where traits are randomly distributed across species, TADs should approach a Poisson lognormal distribution with an excess of rare species (Fig. 1). This is consistent with findings that the skewness of SAD may reflect sampling effects as much as biological structure (McGill 2003). Positive trait value–abundance correlations mean that abundant species have higher, and rare species lower, trait values on average. This should cause a more pronounced dominance order and lower evenness in the TAD, while negative correlations should result in higher evenness. The neutral distributions might therefore form a standard to which observed differences in SADs and TADs can be compared. However, surprisingly little is known about empirical TADs and the extent to which they vary from the SAD, for a given community. Our study intends to fill this gap in knowledge.

Here, we explore the role of subordinates in plant community assembly using an exceptionally large Palaearctic dataset, the GrassPlot database (Dengler et al. 2018, Biurrun et al. 2019, 2021). These data cover diverse site conditions and management regimes of open vegetation across western, central, and eastern Europe, allowing for the study of dominance orders of SADs and TADs and enabling the differences in these to be related to community trait abundance, functional diversity, and compositional stability (Ulrich et al. 2022). The main aims of the presented study are to assess: 1) the difference in trait abundances between dominant and subordinate species, and 2) the importance of environmental factors on subordinate trait distributions. We focus on the questions of what the importance of subordinate species is in overall community functional diversity, and whether dominants and subordinates are functionally similar in accordance with the insurance hypothesis. Using appropriate environmental data, we finally ask how environmental conditions shape the spatial distribution of subordinate species.

## Material and methods

### Vegetation–plot data

Using a minimum richness threshold of 20 plant species per plot, we extracted data from 10-m<sup>2</sup> plots across the European part of the GrassPlot database (Dengler et al. 2018, Biurrun et al. 2019, <https://edgg.org/databases/GrassPlot>). The lower richness boundary of 20 species allows for a sound assessment of the numbers and identities of abundant, subordinate and rare species. For comparability of dominance structures, we restricted our study to 1224 plots from the widely distributed *Festuco-Brometea* phytosociological class (semi-dry and dry grasslands). In order to avoid potential spatial autocorrelation, we always removed one plot in cases of ‘sibling’ plots, where two 10-m<sup>2</sup> plots were included in two opposite corners of a 100 or 1000 m<sup>2</sup> plot. Finally, we removed all plots with < 95% trait coverage of dominant and subordinate species. This strict plot and species selection left 932 plots from 12 countries (Supporting information). These plots contained a total of 1879 vascular plant species.

Abundances for all species in a plot were assessed by the percentage cover (Chiarucci et al. 1999, Anderson et al. 2012) because cover data are often more strongly correlated with plant biomass than with the number of ramets, that is, single shoots (Chiarucci et al. 1999). Total plant cover was the sum of all plant cover data.

### Climate and soil variables and plant traits

To assess potential environmental drivers behind the observed changes in community composition we extracted four important climate variables from the geographic coordinates of each plot using the European WorldClim ver. 2.1 bioclimate data (Fick and Hijmans 2017) and EnviDat (Karger et al. 2020): minimum temperatures of the coldest month ( $T_{\min}$ ), temperature seasonality ( $T_{\text{seasonality}}$ ), precipitation of the driest month ( $P_{\min}$ ), and precipitation seasonality ( $P_{\text{seasonality}}$ ). For the extraction of variables, we used the ‘geodata’ and ‘raster’ R packages (Hijmans 2023, Hijmans et al. 2024). The climate variables were correlated with plot longitude, but less with latitude, and thus indicate a gradient towards increasing climate continentality (Supporting information). For 529 plots, data on soil depth, and for 931 plots, data on elevation were available along with GrassPlot data. Soil depth ranged from 0.8 to 106.0 cm (Supporting information).

We used the BIEN, FloraVeg.EU, TRY, the Pannonian and Ukrainian plant trait databases (Enquist et al. 2016, Kattge et al. 2020, Sonkoly et al. 2023, Chytrý et al. 2024, Vynokurov et al. 2024), the Seed Information Database (SER 2023), and the SLA database (Utkin et al. 2022) to source data (where available) on three important functional traits for each species: specific leaf area (SLA), plant height (PH), and seed mass (SM). These traits are closely related to plant production and fitness (Aerts and Chapin 1999, Reich et al. 1999, Ryser and Urbas 2000) and are commonly used to assess plant community functioning (Kazakou et al. 2014, Mudrák et al. 2019). For the analyses, we discarded all plots where more than 5% of the dominant and subordinate

species had no recorded value of a focal trait. This restriction left 282 plots for SLA, 582 plots for seed mass, and 792 plots for plant height. Trait and environmental data of each plot are contained in the Supporting information.

### Data analysis

For each trait and species, we calculated the total trait abundance ( $t_i$ ) as  $t_i = \tau_i c_i$ , where  $t_i$  and  $c_i$  denote the trait value ( $\tau$ ) and abundance value ( $c$ , estimated from the plant cover) of species  $i$ , respectively. We used Pearson correlations ( $r_{c,t}$ ) to assess the relationship between  $c$  and  $t$  at the plot scale. We then compared the resulting species trait (TAD) and species abundance (SAD) distributions at the plot level. For each plot, we calculated the relative abundance of all middle ranking 50% of species, the subordinate species ( $p_A = \sum c_i(\text{subordinate})/C$ ) and, separately for each trait, the relative subordinate trait abundance ( $p_T = \sum \tau_i(\text{subordinate})/T$ ), where  $C$  and  $T$  denote the total plant cover and trait abundance of that plot, respectively. We also calculated separately for each plot and trait the Spearman’s rank correlations  $r_A$  between  $t$  and  $c$ .

To assess the importance of subordinate species with respect to community functional diversity we used three approaches. First, we calculated Spearman’s rank order correlations ( $r_S$ ) between the SAD and the TAD for dominant and subordinate species. We then calculated the degree of Pielou evenness for each SAD and TAD using the exponential form  $E_p = e^H/S$ , with  $H$  being Shannon diversity and  $S$  the species richness. We compared TADs and SADs using the difference  $\Delta E_p = E_p(\text{TAD}) - E_p(\text{SAD})$ . A positive  $\Delta E_p$  indicates a higher evenness of the TAD in line with a negative  $r_S$  correlation and comparatively higher trait values of rare species (Fig. 1). Finally, for each trait and category, we calculated Rao’s quadratic entropy  $FD_Q$ , an abundance based metric that quantifies the degree of functional diversity (Botta-Dukát 2005).

These approaches are constrained by the non-independence of cover data and depend on species richness. Therefore, we used a null model approach and compared the observed values (obs) of  $r_S$ ,  $E_p$ , and  $FD_Q$  with those expected (exp) after an equiprobable reshuffling of trait values across species identities (9999 replications each). We then used standardised

effect sizes  $SES = \frac{\text{obs} - \text{exp}}{\tilde{A}_{\text{exp}}}$  with  $\sigma_{\text{exp}}$  being the SD of the

null distribution (see Bernard-Verdier et al. (2012) for a similar approach). Trait values and abundances were normalised at the plot level in the range of [0,1] before calculations. Average values of all raw and SES transformed metric values, together with SEs, median and quartiles, are contained in the Supporting information.

To assess differences in trait space between dominant and subordinate species we calculated for each trait  $\times$  plot combination the functional trait diversity (FD) of dominant and subordinate species separately. FD was calculated as the mean Euclidean distance in trait space between all pairs of species which occurred in each plot. We then counted how often the difference  $\Delta FD = FD_{\text{subordinate}} - FD_{\text{dominant}}$  was larger or smaller than zero. Negative  $\Delta FD$  values indicate that the functional

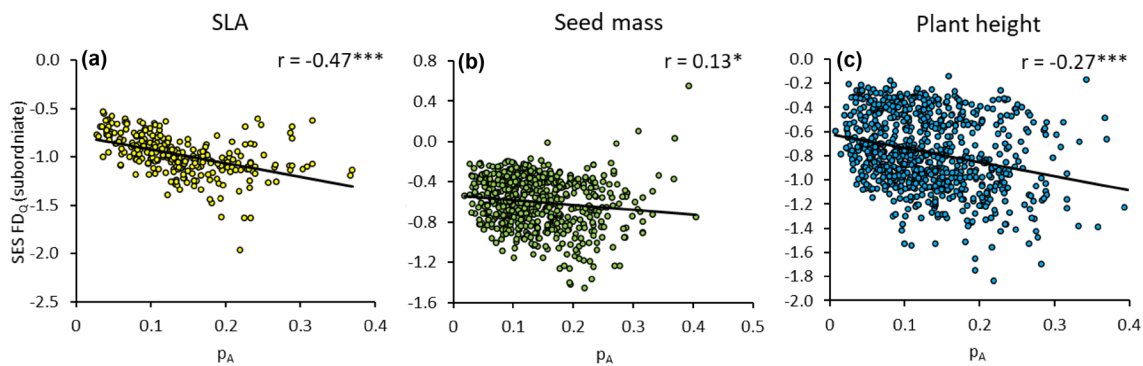


Figure 2. Dependence of standardised effect sizes of subordinate functional diversity (SES  $FD_Q$ ) on the proportion of total plant cover represented by subordinate species ( $p_A$ ), for (a) SLA, (b) seed mass, and (c) plant height. Significance of Pearson correlation coefficients: \* $p(F) < 0.05$ , \*\*\* $p(F) < 0.001$ .

diversity of dominant species is larger than that of subordinate species, and vice versa.

To answer our second starting question (i.e. the extent to which subordinate trait distributions depend on environmental characteristics), we used main effects generalised linear models (identity link function, normal error structure and maximum likelihood estimation) to relate the SES values of  $p_A$ ,  $p_T$ ,  $E_p$  and  $FD_Q$  as response variables to plot elevation, soil, and climate data. Plot richness and plant cover served as metric covariates, and country as a categorical covariate, the latter to assess the influence of spatial non-independence on the abundance distributions. In the models for  $p_T$ ,  $E_p$  and  $FD_Q$  we were particularly interested in the effects of climate and soil and therefore we removed country from the models because of the covariance with the climate variables. Plant cover served as co-variate because of its influence on trait abundance (van der Merwe et al. 2021). All predictor variables were z-transformed prior to analyses. Predictor variables were at most moderately correlated (all Pearson's  $r$  values  $\leq 0.71$ ; Supporting information). Data were likely autocorrelated to a certain degree. However, we did not directly account for this (for instance using spatial eigenvectors), because we either used country as a covariate that accounted for most of the associated variance (in the model for  $p_A$  as response), or we were interested in the effects of the environmental variables that would otherwise be partly hidden in the variance of the spatial eigenvectors. We also did not include interaction terms due to frequent sample size limitations (Duncan and Kefford 2021). Statistical calculations were undertaken using IBM SPSS Statistics ver. 29. Metric values and the associated standardised effect sizes were calculated from the raw data using Fortran code, available from the first author on request.

## Results

### Basic relationships

The plots contained  $39 \pm 1$  species on average ( $\pm$  SE). Among the plots, trait spaces for SLA, seed mass, and plant

height of subordinates tended to be smaller than those of dominants (Supporting information). The proportion of total plant abundance represented by the subordinate species ( $p_A$ ) did not exceed 50% for any plot (Fig. 2), with a median of 11.9% (lower quartile 7.6%, upper quartile 17.4%). The fraction of total trait abundance covered by the subordinate species ( $p_T$ ) was also low, with a median of  $< 20\%$  for all three traits, although in a few cases for seed mass reaching  $> 90\%$  (Supporting information). Species and trait abundances of subordinate species of all three traits were positively correlated, although only weakly ( $r = 0.24$ ) in the case of seed mass (Supporting information).

For all three traits, the standardised effect sizes of functional diversity ( $FD_Q$ ) of dominant grassland species were significantly higher than expected from a standard normal distribution ( $p < 0.001$ ), and also significantly larger than the values for subordinate species, the latter being lower than expected by the null model (Fig. 3a). The species rank orders of SADs and TADs of subordinates ( $r_s$ ) were significantly negatively correlated (Fig. 3b); for dominant species this was only the case for SLA (Fig. 3b). The evenness of the TADs of all three traits ( $\Delta E_p$ ) was on average higher than those of the respective SADs (Fig. 3c). In the case of SLA, raw species trait values and abundances were on average negatively correlated among plots ( $r_{c,\tau} = -0.10 \pm 0.01$ , not shown), and for seed mass and plant height positively correlated on average ( $r_{c,\tau} = 0.07 \pm 0.01$  and  $r_{c,\tau} = 0.06 \pm 0.01$ , respectively).

Total subordinate trait abundance tended to increase with species richness for SLA and seed mass (Supporting information). The normalised functional diversity of subordinates (SES  $FD_Q$ ) tended to decrease with increasing plot richness, particularly with respect to SLA and plant height (both  $p < 0.01$ ; Supporting information). Dominant species showed the opposite pattern: moderate positive correlations between SES  $FD_Q$  and richness (SLA:  $r = 0.25$ ,  $p < 0.01$ ; seed mass:  $r = 0.02$ ,  $p > 0.1$ ; height:  $r = 0.08$ ,  $p < 0.05$ ). The  $r_s$  and  $\Delta E_p$  values of subordinates were only weakly correlated with species richness (Supporting information). Both tended to decrease with increasing richness for seed mass (Supporting information).

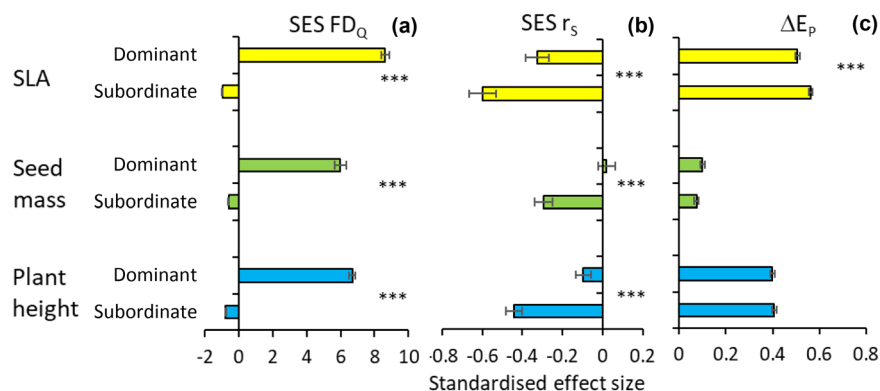


Figure 3. Mean values of standardized effect sizes ( $\pm$  SEs) of (a) functional diversity (SES  $FD_Q$ ), (b) the TAD–SAD correlation (SES  $r_s$ ), and (c) the difference in the evenness between the TAD and the SAD ( $\Delta E_p$ ). Data are for SLA (yellow), seed mass (green), and plant height (blue). Significance for each trait refers to comparisons of dominant and subordinate species using t-tests with  $***p(H) < 0.001$ .

### Environmental correlates

Temperature and precipitation in combination with country identity appeared to be the most important explanatory variables of the proportion of subordinate abundance ( $p_A$ ) in the generalised linear models ( $p_A$ ; Fig. 4). Lower minimum temperatures and higher climatic seasonality ( $T_{\text{seasonality}}$ ) decreased this abundance (Fig. 4). There was also a signal of increasing subordinate abundance at higher elevation in the model including country as a covariate, while soil depth did not have a significant influence (Fig. 4).

The four climatic variables were significantly positively or negatively correlated with the proportion of subordinate trait abundance ( $p_T$ ; Fig. 5a, d, g, Supporting information). Precipitation was the major negative driver of subordinate trait abundance of SLA and plant height (Fig. 5a, d), while for seed mass, temperature played this role (Fig. 5d). Higher minimum precipitation was positively correlated with subordinate plant height (Fig. 5g). For SLA and seed mass, but not for plant height,  $\Delta E_p$  was only weakly related to the environmental drivers (Fig. 5b, e, h). Higher  $T_{\text{seasonality}}$  and  $P_{\text{seasonality}}$  increased SES  $\Delta E_p$  of seed mass. Subordinate functional diversity (i.e. SES of  $FD_Q$ ) was consistently negatively correlated with  $T_{\text{seasonality}}$  (Fig. 5c, f, i). Higher  $P_{\text{seasonality}}$  increased SLA functional diversity (Fig. 5c). Subordinate functional diversity of all three traits decreased with elevation, significantly so ( $p < 0.001$ ) with respect to plant height (Fig. 5c, f, i).

### Discussion

Our work primarily aimed to infer the functional importance of subordinate species in European grassland communities. Our study is, to our knowledge, the first to use and compare trait abundance distributions in order to assess the role of subordinate species in grassland communities. We found consistent and statistically significant positive correlations between species trait abundance ( $p_T$ ) and relative abundances ( $p_A$ ; Supporting information). We also found a reordering of species ranks from SADs to TADs in dominant and subordinate species (Fig. 3b). Although we expected to see most

subordinate species (classified based on abundance) to also be included in the subordinate group with respect to the TAD, this was not the case, particularly for SLA. These results suggest differential plant community assembly patterns between dominants and subordinates, indicating underlying community assembly processes that appear to be non-random regarding trait assembly.

We found a significant reordering of species rank orders of dominant and subordinate species when comparing SADs and TADs (Fig. 3). This finding calls for a reassessment of the importance of TADs in ecological research. Comparative ranking according to species traits has frequently been proposed to quantify community functioning (Chiarucci et al. 1999, Jain et al. 2014, Laughlin et al. 2015). However, this

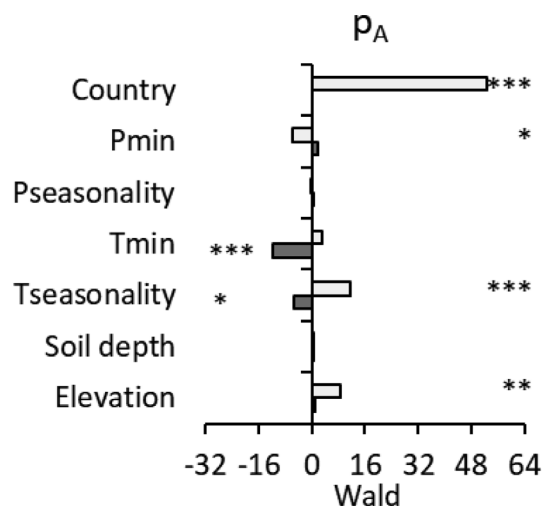


Figure 4. Summary results (Wald statistics) of main effects generalised linear models with the proportion of total abundance represented by subordinate species ( $p_A$ ) as the response variable. Positive or negative Wald values indicate the direction of influence inferred from the associated sign of the model parameters. Country served as a categorical covariate in some models: light grey bars relate to the model including, and dark grey bars to the model excluding, country as a covariate.  $n = 522$ . Wald  $\chi^2$  significances: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

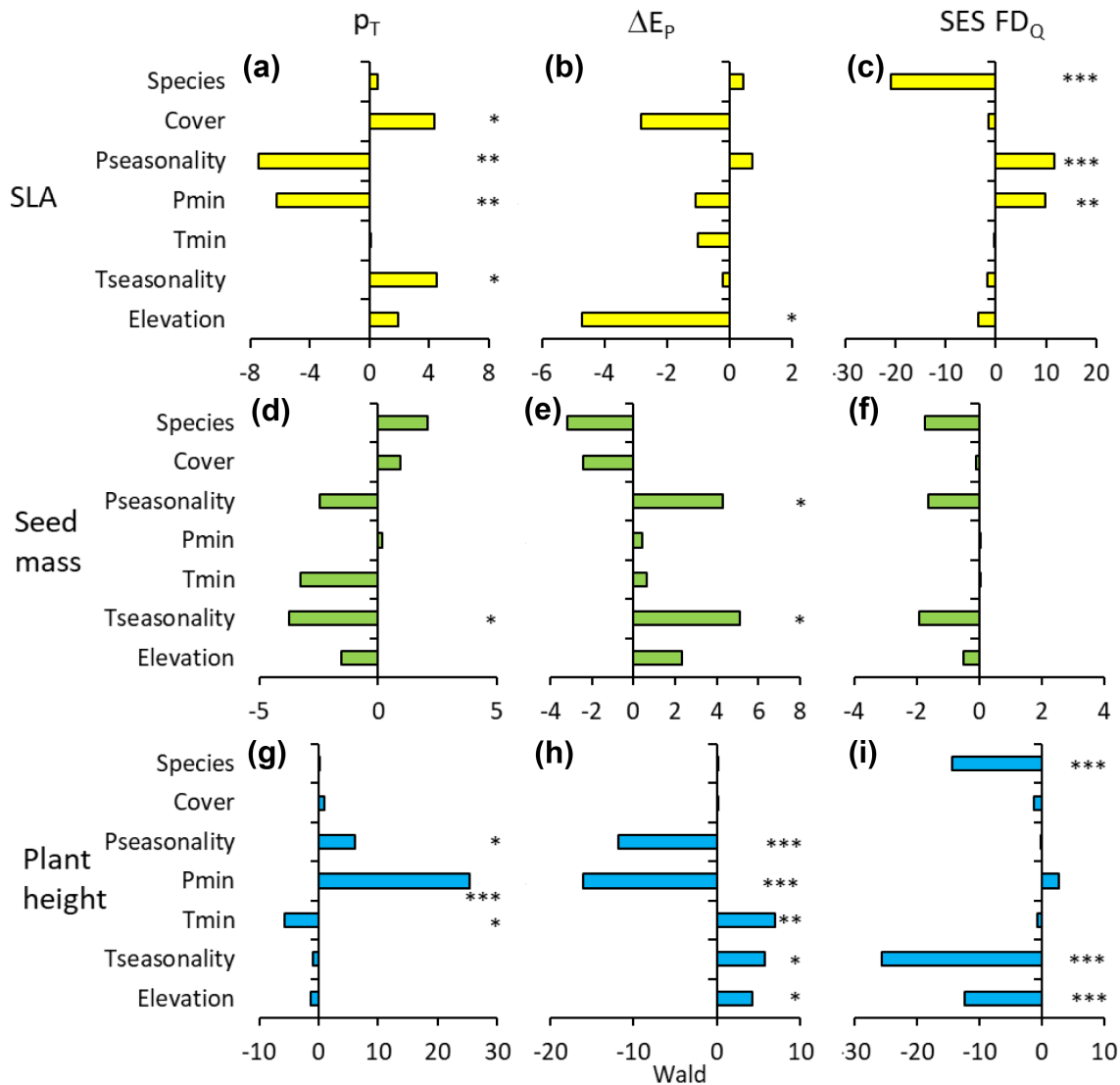


Figure 5. Summary results (Wald statistics) of main effects generalised linear models with (a, d, g) the proportion of subordinate trait abundance ( $p_T$ ); (b, e, h) difference in evenness between TADs and SADs ( $\Delta E_p$ ); and (c, f, i) subordinate functional diversity (SES  $FD_Q$ ) as response variables. Positive or negative Wald values indicate the direction of influence inferred from the associated sign of the model parameters. Complete model results are contained in the Supporting information.  $n=281$  (SLA), 568 (seed mass), 770 (plant height). Wald  $\chi^2$  significances: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

has mainly been undertaken directly at the trait level by comparisons of trait ranking across time and space (Garnier et al. 2001, Kazakou et al. 2014). Here, we propose to calculate TADs directly and to compare SADs and TADs to infer patterns of community assembly from a trait perspective (see Koffel et al. 2022 for a related approach).

With respect to our second starting question, we found that the functional diversity (SES  $FD_Q$ ) of subordinate species was, in the majority of plots, smaller than that of dominant species (Fig. 3a, Supporting information), in line with the view that dominant species contribute most to ecosystem functioning (Jain et al. 2014, Leitão et al. 2016). This pattern was accompanied by the generally higher evenness of the TADs in comparison to SADs (Fig. 3c). We were surprised to find that the functional diversity of subordinates

was consistently lower than expected by chance, a pattern not seen in the dominant species (Fig. 3a). This finding indicates that contrary to the insurance model subordinates might not be fully able to take over functions from disappearing dominant species, at least not immediately (Soliveres et al. 2015).

Our null model approach largely removed the dependence of our dominance measures on species richness (Fig. 5). Nevertheless, the functional diversity of subordinates still tended to decrease with increasing species richness (Fig. 5, Supporting information). This finding contradicts the common view about a general positive relationship between species richness and functioning (for counterexamples see: Kenkel et al. 2000, Hooper et al. 2005, Creed et al. 2009, Lepš 2013). In this respect, Kazakou et al. (2014) reported a high variability when comparing abundance based and SLA

based species rankings for individual herbaceous plant species across different ecosystems. This finding would imply frequent independence of functional and species diversity. On the contrary, our results are parsimoniously explained by a pattern of community assembly, where dominant species exhibit similar values of SLA and diversity irrespective of community richness. Subordinates, being, by the definition employed in this study, always twice as species rich, also have a higher probability of occupying a wider trait space that increases at a low rate with increasing richness. Indeed, [Barga et al. \(2018\)](#) reported that co-occurring subordinate forbs often exhibit contrasting climate niches. Because SLA is known to change with climate niche ([Dwyer et al. 2014](#)), this should translate into a comparatively large subordinate functional diversity. Our explanation is also in line with [Arnillas et al. \(2021\)](#), who found that dominant grassland species tend to be phylogenetically clustered with a higher probability to exhibit similar traits, while non-dominants were phylogenetically overdispersed. Future studies should look more closely at the scaling of functional diversity and the abundances of dominant and subordinate species.

We found that the functional roles of subordinate species vary across countries and climatic regimes. Our data mainly came from western and central European mountain regions and eastern European lowlands (Supporting information). Country differences may reflect variations in local management regimes and national conservation policies ([Napoleone et al. 2022](#)). Climatic conditions span a longitudinal gradient towards a continental climate regime with pronounced seasonality and colder winters, and a latitudinal gradient linked to a decrease in summer drought at higher latitude. Therefore, the use of elevational range and climatic variability as predictors should have been sufficient to detect any dependencies of subordinate trait distributions on climate parameters. Indeed, pronounced climate seasonality tended to reduce subordinate species abundances and trait abundance ([Fig. 4–5](#)). Thus, the shape of both the species abundance and trait abundance distributions, at least for grassland plants, are seemingly related to climatic conditions. While previous studies have found an influence of various environmental factors, including climate, on the SAD ([Arellano et al. 2017](#), [Matthews et al. 2019](#), [Ulrich et al. 2022](#)), the extent to which climate affects both the SAD and TAD in tandem is poorly known. Gaining this understanding will likely be important in developing a fully mechanistic understanding of abundance distributions and community assembly ([Van der Putten et al. 2010](#)). Our results imply that the functional roles of subordinate species vary as a function of the climatic regime; if true, this would have broad implications for theories about community assembly and complementarity ([Grime 1998](#), [Yachi and Loreau 1999](#), [Sasaki and Lauenroth 2011](#)).

As a side effect, our results revealed the more even distribution of the TAD in comparison to the SAD. This finding is likely related to the more equal, or even higher, resource use of subordinate and rare species than indicated by the species' relative abundances ([Fig. 1](#)). This finding has implications for

the assessment of the strength of competitive relationships from relative abundances ([Hart et al. 2018](#)). Our results strongly indicate that realised competitive interactions might be less severe than suggested by the SAD. Importantly, the  $\Delta E_p$  values of subordinates for SLA were significantly larger than for dominant species, indicating a shift towards more equal plant growth in this group ([Fig. 3](#)). Further studies are needed to reveal whether and why TADs of plant communities are frequently more even than SADs.

Climatic seasonality increases at higher elevation. Our interpretation of the role of climatic seasonality is therefore also corroborated by the negative effect of elevation on subordinate functional diversity ([Fig. 5](#)). With this exception, elevation did not significantly affect subordinate abundances and trait abundance ([Fig. 4–5](#)). This is again a sign that SADs and TADs convey distinct information and that both distributions need to be evaluated for a full understanding of plant community assembly.

We were surprised that soil depth appeared to be of less importance for subordinate species ([Fig. 4](#)). This lack of a significant relationship contrasts with previous findings related to trait abundance along soil depth gradients, where SLA and seed mass both showed strong responses to different soil depths ([Bernard-Verdier et al. 2012](#)). Unfortunately, studies relating subordinate trait abundances to soil variables are largely missing. One exception is the study of [LaPlante and Souza \(2018\)](#), which found that the subordinate diversity of mountain meadows was likely driven by abiotic factors rather than by competitive interactions with dominant species. Our results do not corroborate these or the results of [Bernard-Verdier et al. \(2012\)](#), as the effect sizes we report here were only small and in the majority of comparisons non-significant despite the comparatively large number of plots. Similarly, they also do not corroborate [Rodríguez et al. \(2023\)](#), who reported soil properties to be the main drivers of grassland plant functional diversity. Although our study focused on a single phytosociological class, semi-dry and dry grasslands of the class *Festuco-Brometea*, the plots covered a large geographic region, including western, southern, central, and eastern Europe with very different soil, and particularly aridity, conditions. Because soil factors might act differently on community assembly and trait abundance, the relationship between dominant and subordinate species and soil depth might also be too complex to be detectable with linear models.

## Conclusions

Our study highlights the role of subordinate species in grassland plant communities. Through analysis of trait abundance distributions, we found that the contribution of subordinates to total plant community functional diversity exceeded on average their relative abundance, although it was less than expected from a random sample according to our null model. Our results reveal differences in trait abundance between dominant and subordinate species. For the Palearctic *Festuco-Brometea* grasslands, the main drivers of subordinate

abundance, trait abundance, and functional diversity are climate seasonality and, depending on the trait, elevation. Our results call for more comparative studies looking at how subordinate species and their associated functional traits vary along gradients of environmental conditions. Subordinates should not remain a neglected group.

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### Author contributions

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### Data availability statement

Data are available from the GrassPlot database: <https://edgg.org/databases/GrassPlot>.

### Supporting information

The Supporting information associated with this article is available with the online version.

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