

RESEARCH ARTICLE

Soil conditions drive below-ground trait space in temperate agricultural grasslands

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Funding information

Deutsche Forschungsgemeinschaft,
Grant/Award Number: 323522591 and KL
1866/12-1; Research Foundation

Handling Editor: Marina Semchenko

Abstract

1. Plant below-ground organs perform essential functions, including water and nutrient uptake, anchorage, vegetative reproduction and recruitment of mutualistic soil microbiota. Recently, multivariate analyses showed that root traits of species can largely be linked to a 'conservation' and a 'collaboration' gradient. Here, we tested whether this species-level bidimensional below-ground trait space also exists at the community level in grasslands. Furthermore, we tested whether the position of grassland communities in below-ground trait space relates to environmental variables.
2. For a total of 313 species, we collected data on eight below-ground traits in greenhouse and common garden experiments and supplemented it with data on bud-bank size and specific leaf area from databases. We calculated community weighted means (CWMs) of these 10 traits for 150 temperate grassland plots to investigate below-ground plant-trait dimensionality and its variation along 10 soil and land-use parameters.
3. Using PCA, we found that about 55% of variance in CWMs was explained by two main dimensions, corresponding to a mycorrhizal 'collaboration' and a resource 'conservation' gradient. Frequently overlooked traits such as rooting depth, bud-bank size and root-branching intensity were largely integrated in this trait space. The two plant-strategy gradients were partially dependent on each other, with communities that do 'outsourcing' of resource uptake to mycorrhizal fungi along the collaboration gradient also being more 'slow' along the conservation gradient. (i.e. high root tissue density and high root weight ratio). 'Outsourcing' communities were also more often deep rooting and associated with soil parameters, such as low moisture and sand content, high topsoil pH, high C:N and low $\delta^{15}\text{N}$.

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'Slow' communities had large bud banks and were associated with low land-use intensity, high topsoil pH and low nitrate but high ammonium concentration in the soil. Surprisingly, we did not find an association of phosphorus availability with the mycorrhizal 'collaboration' gradient.

4. *Synthesis*. The 'collaboration' and 'conservation' gradients previously identified among species scale up to the community level in grasslands, encompass more traits than previously described, and vary with the environment.

KEYWORDS

bud-bank traits, environmental filtering, land-use, mycorrhiza, nitrogen, phosphorus, plant economics spectrum, root traits

1 | INTRODUCTION

Plant traits are of major interest as they determine plant functioning (Solbrig, 1993), covary with environmental conditions (Garnier et al., 2016), and influence ecosystem functions (de Bello et al., 2010; Hanisch et al., 2020). Nevertheless, traits frequently have low predictive power (Klimešová et al., 2016; van der Plas et al., 2020), because there is limited understanding of which and how many traits are needed in ecological studies (Shingley et al., 2016). An important step forward has been the grouping of multiple traits into a limited number of syndromes, with continuous variation in the form of plant-strategy gradients (Bergmann et al., 2020; Chave et al., 2009; Díaz et al., 2016; Klimešová, Martínková, & Herben, 2018; Pierce et al., 2013; Roddy et al., 2020; Westoby et al., 2002; Wright et al., 2004). For example, Díaz et al. (2016) showed that variation in above-ground traits can be captured by a 'size' gradient representing the size of whole plants and plant organs, and an 'economic' gradient representing the leaf economics spectrum. Similar attempts have recently addressed variation in root traits and identified a 'conservation' gradient and a 'collaboration' gradient as two independent axes of below-ground plant economy (Bergmann et al., 2020; Kramer-Walter et al., 2016; Weemstra et al., 2016).

Bergmann et al. (2020) suggested that in the root economic space the 'conservation' gradient, ranging from 'slow' to 'fast', is related to carbon conservation and determined by root tissue density and nitrogen (N) content. In contrast, the 'collaboration' gradient, ranging from 'do-it-yourself' to 'outsourcing' of resource uptake to fungal partners, is reflected by specific root length and root diameter along with mycorrhizal colonization (Figure 1a). Despite this recent progress, several root traits with a potentially high importance for plant functioning (Laliberté, 2017) have not been integrated into the existing framework yet. For example, a high root-branching intensity could be an alternative to the reliance on mycorrhiza, and may be associated with a high specific root length for better soil exploitation (Kong et al., 2014; Freschet et al., 2020; Ding et al., 2020). Thus, a high root-branching intensity and high specific root length may both be indicative of a 'do-it-yourself' strategy. Rooting depth is also considered to be an important trait (Mommer et al., 2010; Mueller

et al., 2013), while variation therein seems to be independent from collaboration and conservation strategies (Díaz et al., 2016; Weigelt et al., 2021). On the one hand, herbaceous species with superficial root systems, such as crops growing on highly fertile topsoils (Thorup-Kristensen et al., 2020) are considered to have a 'fast' strategy. On the other hand, as species with deep roots are able to take up nutrients and water from deeper soil layers, those species might also have a 'fast' strategy (Figure 1a). Further integration of these root traits in the below-ground trait space is needed for a comprehensive understanding of the plant-soil interface.

Below-ground organs other than roots add another layer of complexity in terms of form and function to the plant-trait space. Rhizomes, root buds and tubers play important roles in storage and vegetative reproduction (Klimešová, Martínková, & Ottaviani, 2018). Species with a large bud-bank size are more likely to be perennial and 'slow' growing (E-Vojtkó et al., 2017). Furthermore, although not strictly a below-ground trait, the root weight ratio, that is, the proportion of biomass allocated to roots, is a useful indicator of plant investment into the uptake and storage of different resources (Reynolds & D'Antonio, 1996). According to the Optimal Partitioning Theory, plants should allocate biomass to the organ that acquires the most limiting resource (Bloom et al., 1985). When soil resources are abundant, investment in roots usually decreases in favour of above-ground organs, and a low root weight ratio could thus indicate a 'fast' strategy where few roots are needed for a high uptake capacity of nutrients (McCarthy & Enquist, 2007). As a high investment in roots may allow for deeper roots and more root buds, the root weight ratio may additionally be linked to rooting depth (Schenk & Jackson, 2002a) and bud-bank size. It remains to be tested whether these below-ground traits are aligned with the 'conservation' or 'collaboration' gradient, or rather represent independent gradients.

The few studies on below-ground traits and their variation along environmental gradients are generally limited to root morphological traits and only use a limited set of coarse environmental parameters (Craine et al., 2001; Erktan et al., 2018; Prieto et al., 2015). Analyses of the relationships between above-ground traits and various types of environmental factors, such as climate, soil properties and land-use intensity, have already improved our

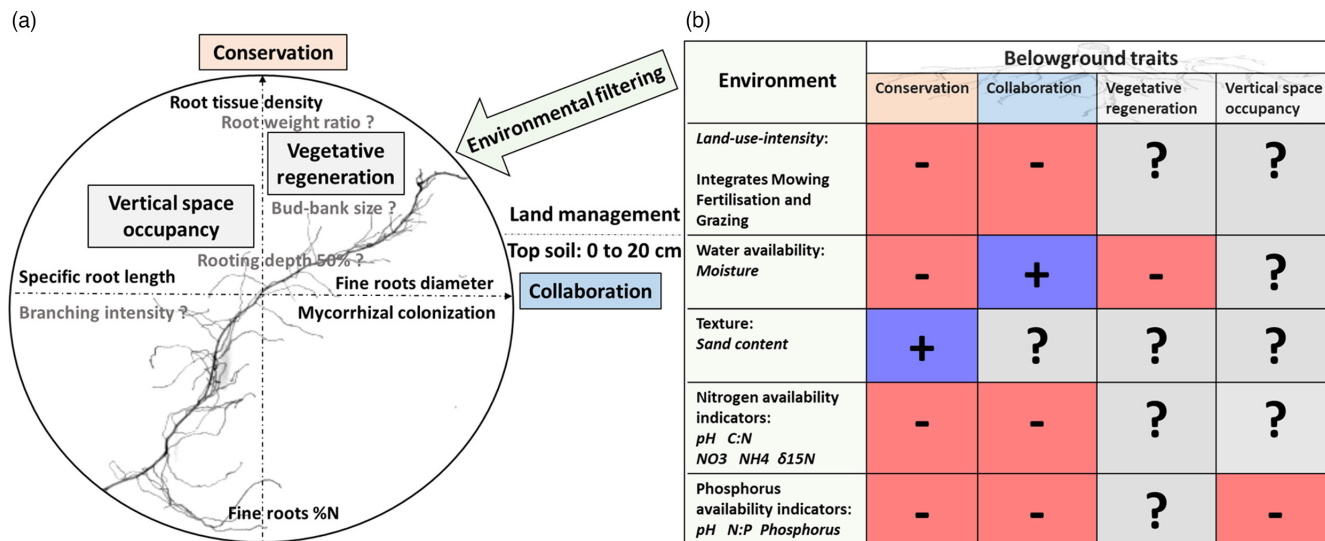


FIGURE 1 Hypothesized relationships between (a) community weighted means (CWMs) of below-ground traits in grasslands aligned on two potential plant-strategy gradients. A ‘conservation’ and a ‘collaboration’ gradient are expected as the main dimensions of plant variation, as our trait selection contains mostly traits of the root economics space. A ‘vegetative reproduction’ and ‘vertical space occupancy’ aspect could represent additional plant-strategy gradients, or be embedded within the ‘conservation’ and ‘collaboration’ gradients. The two known below-ground dimensions are represented as two orthogonal axes (‘conservation’ and ‘collaboration’) with the traits that have been previously shown to be associated with them in black font. The positions of four other traits, bud-bank size, root weight ratio, branching intensity and rooting depth 50% (grey font), are yet unknown. (b) As a result of environmental filtering, each plant-strategy gradient could be associated with different environmental variables. The signs and colours indicate the hypothesized directions of the relationships. The references on which these hypothesized relationships are based can be found in [Appendix S4](#)

understanding of trait variation in grasslands (Garnier et al., 2007), and should also be applied to below-ground traits. In particular, plants may have various strategies to deal with nutrient deficits and imbalances in soils. For example, it is likely that mycorrhizal collaboration becomes more important in soils with limited phosphorus (P) availability (Ma et al., 2020). Similarly, the form of plant-available mineral soil N (ammonium vs. nitrate) could also select for different below-ground traits, as species vary in their preference for different forms of N (Maire et al., 2009; Pordon et al., 2007; Weigelt et al., 2005).

To better understand how below-ground plant traits relate to environmental variation, we investigated (1) how community weighted means (CWMs) of different below-ground traits align along known plant-strategy gradients, and (2) how the shifts of CWMs along these strategy gradients depend on environmental variables. Thus, we complemented traits known to define the gradients of the root economics space with additional below-ground traits that might represent independent strategies of plant functioning. Therefore, we used species traits that we measured on plants grown in pots or extracted from databases. We combined these trait data with vegetation-relevé data from 150 grassland plots in Germany to calculate CWMs of a total of 10 traits. We then assessed the dimensionality of the variation in these CWMs with principal component analysis (PCA) and related the principal components to 10 land-use intensity and soil variables. A priori hypotheses on the relationships between traits, plant-strategy dimensions and environmental variables are presented in [Figure 1](#).

2 | MATERIALS AND METHODS

2.1 | Data on grassland vegetation composition

The plant-community data used as a baseline for Central European agricultural grassland vegetation originate from the ‘Biodiversity Exploratories’ project (Fischer et al., 2010). In each of three regions of Germany, the Schwäbische-Alb (south-western Germany), Hainich-Dün (central Germany) and Schorfheide-Chorin (north-eastern Germany), 50 grasslands covering a wide range of land-use intensities were selected. From 2008 to 2019, the vegetation composition of a 4 m × 4 m plot in each of the 150 grasslands was assessed annually in May/June by identifying all vascular plant species and visually estimating their above-ground cover. To align the species names between the vegetation and trait datasets, we standardized the species names according to the accepted names in The Plant List (www.theplantlist.org, accessed 15 June 2019, using the TAXONSTAND R package (Cayuela et al., 2012). In total, 319 vascular plant species have been identified in the 150 grassland plots.

2.2 | Plant species traits

We obtained mean species values for eight traits from four pot experiments that we performed, and for two further traits from already existing databases. For 291 of the 319 grassland species, we were able to obtain seeds from commercial seed suppliers or

botanical gardens. We then performed four pot experiments to measure species traits. *Taraxacum* spp. are abundant in the grassland plots, though, due to their complex taxonomy, rarely identified at the species level. We here used trait values of *Taraxacum campyloides* for *Taraxacum* spp. The trait values are part of a previously published dataset (Lachaise, Bergmann, Rillig, & van Kleunen, 2021) and an unpublished dataset (Bergmann et al., unpublished data), and comprehensive descriptions of the experiments are provided in Appendix S1. In brief, we did one greenhouse experiment in which we grew 2659 individual plants, representing 216 species, for 4 weeks after which we weighed the roots and analysed scanned images of the roots with WinRHIZO 2017a software (Regent Instruments Inc., Canada) to determine root tissue density, specific root length, fine root diameter, root weight ratio and root-branching intensity (Lachaise, Bergmann, Rillig, & van Kleunen, 2021). Because these traits were measured on young root systems, most of the roots could be considered fine roots with principally a resource uptake function rather than a transport or storage function. We did a second greenhouse experiment using 2007 plants, representing 196 species, to determine the N content of fine roots (fine roots %N) using isotope-ratio mass spectrometry. In a third greenhouse pot experiment, we determined mycorrhizal colonization rates for 225 plants, representing 75 species that are among the most common ones in the grasslands plots (mean cover of 65%, Appendix S3). Six weeks after inoculation with spores of *Rhizophagus irregularis* (Bergmann et al., unpublished data), roots were harvested and washed, and the percentage of mycorrhizal colonization was determined using the line-intersect method (McGonigle et al., 1990). In a fourth experiment, we grew 752 plants, representing 183 species, outdoors in growth tubes to determine the depth above and below which plants have 50% of their root biomass (Rooting depth 50%, see Appendix S1 or Schenk & Jackson, 2002b for the calculation method) for about 16 weeks. In addition, to have an estimate of the below-ground regeneration potential, we extracted bud-bank size, including stem and root-derived buds occurring below-ground or at the soil surface, from the CLO-PLA database (Klimešová et al., 2017) for 313 of the 319 species. Finally, to also have a reliable indicator of the plant communities' acquisitive side of the plant economics spectrum (Allan et al., 2015; Busch et al., 2019), we extracted specific leaf area, the one and only above-ground trait in our analyses, for 279 of the 319 species from the LEDA database (Kleyer et al., 2008).

2.3 | Environmental variables of grassland plots

To relate the different dimensions of variation in trait CWMs to the abiotic environment, we used 10 environmental variables related to land-use intensity and soil conditions. The goal was to capture a relatively independent set of descriptors likely to drive the below-ground functioning of plants. A detailed description of each variable can be found in Appendix S2. We used the land-use intensity index (Blüthgen et al., 2012), which aggregates information on the intensity of mowing, fertilization and grazing, and is a major driver of ecosystem properties (Allan et al., 2015). We used a variety of

physicochemical indicators related to soil fertility of the topsoil (0–20 cm). Soil-moisture content and sand content were measured to capture soil water availability and texture respectively. Soil pH was chosen, as it affects the availability of essential plant nutrients such as P in soils. We used soil extractable NO₃, extractable NH₄ and δ¹⁵N as indicators of soil nitrogen availability and related processes (Kleinebecker et al., 2014; Robinson, 2001), and the C:N ratio as a coarse indicator of stoichiometry and organic matter decomposability (Schachtschabel et al., 1998). We further made use of resin-bag-adsorbed P and the N:P ratio to capture phosphorus availability in soil (Güsewell, 2004). Because soil volume is a central element in soil fertility and root-system distribution, we used data on bulk densities to convert per-mass nutrient concentrations to per-volume concentrations (Appendix S2). Few of the grassland-site descriptors were measured for each of the years for which we had vegetation-composition data (i.e. for the period 2008–2019). However, we tried to maximize the coverage for this period by using all available census dates for these variables (see Appendix S2 for years covered) and averaging the values per plot.

2.4 | Statistical analyses

All the statistics were done using R v 4.0.1 (R Core Team, 2020).

2.4.1 | Community weighted trait means

To characterize the plant communities of each of the 150 grassland plots based on values of functional traits of their species, we calculated community weighted means (CWMs) as.

$$\text{CWM}^{\text{Trait}} = \sum_{j=1}^S p_j \text{Trait}_j.$$

Here p_j is the relative above-ground cover of species j in the community, Trait_j is the trait value of species j and S is the number of species in the community with available trait data. Because some plots had patches of bare soil in some of the annual vegetation surveys, and because for some species trait data were missing, we normalized plant cover to cumulate to 100% for all species with available trait data in each plot before calculating the CWMs. As trait data for most of the abundant grassland species were available, this analysis includes about 90% of the total plant cover in most plots, for most traits (Appendix S3). The only exception is mycorrhizal colonization, which is only available for 78 species, but, even for that trait, the average cover of species included is 65% (range 32%–87%, Appendix S3).

2.4.2 | Principal components of CWM variation

As the CWMs of several traits were correlated (Appendix S9), we performed PCAs to reduce the dimensionality of the data. To assess

how robust the resulting dimensions are to the inclusion of additional information, we performed four separate PCAs. Each of these PCAs included all nine below-ground traits, but they differed in that we also included or excluded $CWM_{Specific\ leaf\ area}$, as one of the major traits associated with the above-ground 'fast' side of the plant economics spectrum, and that we included or excluded plant functional type information, that is, the percentage cover of grasses (Poales), N-fixing forbs (Fabaceae) and non-N-fixing forbs. So, one PCA included CWMs of below-ground traits only ('Below-ground PCA'), one additionally included $CWM_{Specific\ leaf\ area}$ ('Above-Below-ground PCA'), one additionally included the proportions of Poales, Fabaceae and non-N-fixing forbs, and one included all. To increase the separation of the variable loadings (the trait CWMs) on the two first axes, we performed an 'oblimin' rotation on these axes for the Below-ground PCA and the Above-Below-ground PCA. To complement the information provided on taxonomic or phylogenetic influence on community trait values, we also looked at the 10 most dominant species or taxa in the trait space formed by PC1 and PC2 and the indicator species or taxa that associated with each quadrant of the two-dimensional space formed by PC1 and PC2 (Appendix S13). CWMs are mainly determined by the values of the abundant species in a plot, which may differ in some of their average trait values from less abundant species (Lachaise, Bergmann, Rillig, & van Kleunen, 2021). As measure of abundance, we used the above-ground cover of species which only provides a two-dimensional estimate of abundance (i.e. area instead of volume). Moreover, it has recently been argued that the relative above-ground cover of a species might deviate from its relative below-ground cover (Ottaviani et al., 2020). Therefore, to assess how robust our analyses are with regard to weighting the species trait values, we also did our four PCAs using community arithmetic means (CArMs), where the trait values are not weighted by the species above-ground cover in the community (Appendix S15). Furthermore, to compare the relationships observed at the community level and at the species level, we also did the Above-Below-ground PCA using trait means of the species instead of CWMs (Appendix S14). For each PCA, $CWM_{Root\ tissue\ density}$ was \log_{10} transformed and for each trait or proportion of plant functional type, data were standardized by subtracting the mean and dividing by the standard deviation to conform to the multivariate requirements.

2.4.3 | Associations of the principal components of CWMs with environmental variables

To test for associations between the principal components of CWMs of the grassland plots and the environmental variables, we performed multiple regressions. The PC1 and PC2 scores from each of the four PCAs on CWMs of the functional traits were used as response variables, and the environmental variables were used as predictors. Soil C:N, N:P, sand content, NH_4 , NO_3 and $\delta^{15}N$ were log-transformed before analysis to get a more regular (less clumped)

distribution of the predictor values. To account for the fact that the grassland plots are located in three different regions of Germany, we also included region as a predictor in the models. However, to avoid overfitting of the models, we did not include interactions between regions and other predictors. For model reduction, backward stepwise model selection based on AIC was performed using the function `stepAIC()`. This procedure selects a parsimonious set of predictors while minimizing the variance inflation factor (max VIF = 3.6 for Above-Below-ground PCA). Because the two first axes (PC1 and PC2) of the four PCAs produced similar scores for the CWMs of the grassland plots (all pairwise correlations of the PC1s were >0.98 and those of the PC2s were >0.67), we present the results of the analysis of the 'Above-Below-ground PCA' in the main text (based on the PC axes of Figure 2; see Figure 3), and the results for the other three PCAs in Appendix S7. We did the same for the PC3 to PC6 scores from the Above-Below-ground PCA (Appendix S11), and for each of the 10 CWM_{Traits} (Appendix S12). We further tested if the proportion of the three plant functional types (Poales, Fabaceae, non-N-fixing forbs), as related to the trait dimensions, responded to environmental variables in a similar way.

3 | RESULTS

3.1 | Dimensionality of CWMs

The Above-Below-ground PCA (Figure 2, Appendix S5) and the other three PCAs (Appendices S5 and S6) revealed that the two first axes generally explained about 55%–60% of the total variance in CWMs of traits, and that each of the 10 trait CWMs had intermediate to strong loadings on at least one of these two axes (Appendix S8). PC1 had strong negative loadings of $CWM_{Specific\ root\ length}$ and $CWM_{Branching\ intensity}$, and strong positive loadings of $CWM_{Mycorrhizal\ colonization}$, $CWM_{Fine\ roots\ \%N}$ and $CWM_{Fine\ root\ diameter}$. PC2 had strong positive loadings of $CWM_{Bud-bank\ size}$, $CWM_{Root\ weight\ ratio}$ and $CWM_{Root\ tissue\ density}$, and strong negative loadings of $CWM_{Specific\ leaf\ area}$. PC1 thus overall captured the mycorrhizal 'collaboration' gradient of the root economic space, with the main exception of $CWM_{Fine\ roots\ \%N}$ being positively associated with the other 'collaboration' traits, and PC2 captured the resource 'conservation' gradient. When we used the unweighted CArMs instead of CWMs, PC1 and PC2 largely corresponded to the 'collaboration' and 'conservation' gradients (Appendix S15), indicating that the results are relatively robust with regard to the weighting of the species trait values. The 'collaboration' and 'conservation' gradients, however, were only partially independent (see CWM correlations in Appendix S9) as the 'fast' strategy tended to associate with the 'do-it-yourself' strategy. Furthermore, $CWM_{Rooting\ depth\ 50\%}$ loaded rather strongly on both of these two PCs (Figure 2a; Appendix S8), suggesting that deep-rooting communities were associated with the 'outsourcing' side of the 'collaboration' gradient as well as the 'fast' side of the 'conservation' gradient.

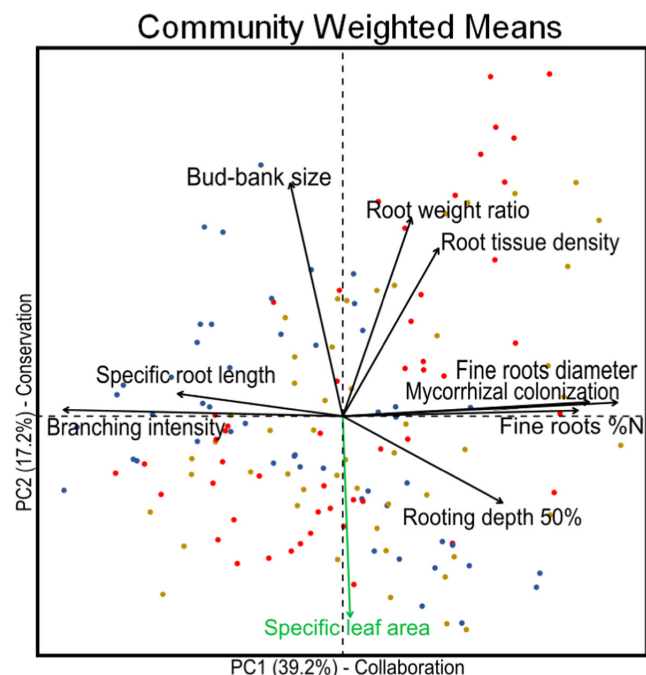


FIGURE 2 The two first principal components (PCs) of the above–Below-ground PCA, explaining 56.4% of the total variance in community weighted means (CWMs). Each CWM_{Trait} has a strong loading on either of the two first PCs (Appendix S8). The subsequent PCs, including PC3 explaining 14.8% of the total variance (Appendix S5), mainly captured variation among the three regions, probably describing differences in regional species pools, but did not strongly relate to any environmental parameter (Appendix S11). The sole above-ground trait that we included, $CWM_{Specific\ leaf\ area}$, is shown in green. The scores of the 150 grassland plots used for the PCA are shown in different colours for each of the three regions (red for the Schwäbische Alb, brown for Hainich, blue for Schorfheide, each with $N = 50$). PC1 is mostly characterized by CWMs of traits related to the mycorrhizal ‘collaboration’ gradient of the root economic space, with on the left, the ‘do-it-yourself’ strategy and on the right, the ‘outsourcing’ strategy. PC2 is more characterized by CWMs of traits related to the ‘conservation’ gradient of a ‘root and leaf economic spectrum’, with at the top, the ‘slow’ strategy and at the bottom, the ‘fast’ strategy. Bud-bank size, as a surrogate of the vegetative regeneration potential, is associated with the ‘slow’ strategy. Correlation coefficients between the CWMs are provided in Appendix S9 and corroborate the relationships observed for PC1 and PC2. The loadings onto PC1 to PC6 (90% of variance explained) are in Appendix S8

3.2 | Associations of the dimensions of CWMs with environmental variables

The positions of a grassland community along the ‘collaboration’ (PC1) and the ‘conservation’ gradient (PC2) were significantly related to several environmental variables (Figure 3). The $\delta^{15}N$ isotopic signal, sand content and moisture of the topsoil were associated with the ‘do-it-yourself’ side of the ‘collaboration’ gradient (i.e. had negative effects on PC1). Land-use intensity and NO_3 content were retained by the model-selection procedure, associating with the

‘do-it-yourself’ side, but their effects were not significant (Figure 3a). The pH and C:N ratio, on the other hand, were associated with the ‘outsourcing’ side of the ‘collaboration’ gradient (i.e. had positive effects on PC1; Figure 3a).

Among the environmental variables, NO_3 content and land-use intensity were significantly associated with ‘fast’ communities (i.e. had negative effects on PC2; Figure 3b). Phosphorus content was also associated with ‘fast’ communities, but this effect was only marginally significant (Figure 3b). NH_4 content and pH, on the other hand, were significantly associated with ‘slow’ communities (i.e. had positive effects on PC2; Figure 3b). The effects and variance explained by the different models are comparable among the four PCAs (i.e. the PCAs with and without $CWM_{Specific\ leaf\ area}$ and with and without the plant functional types; Appendix S6).

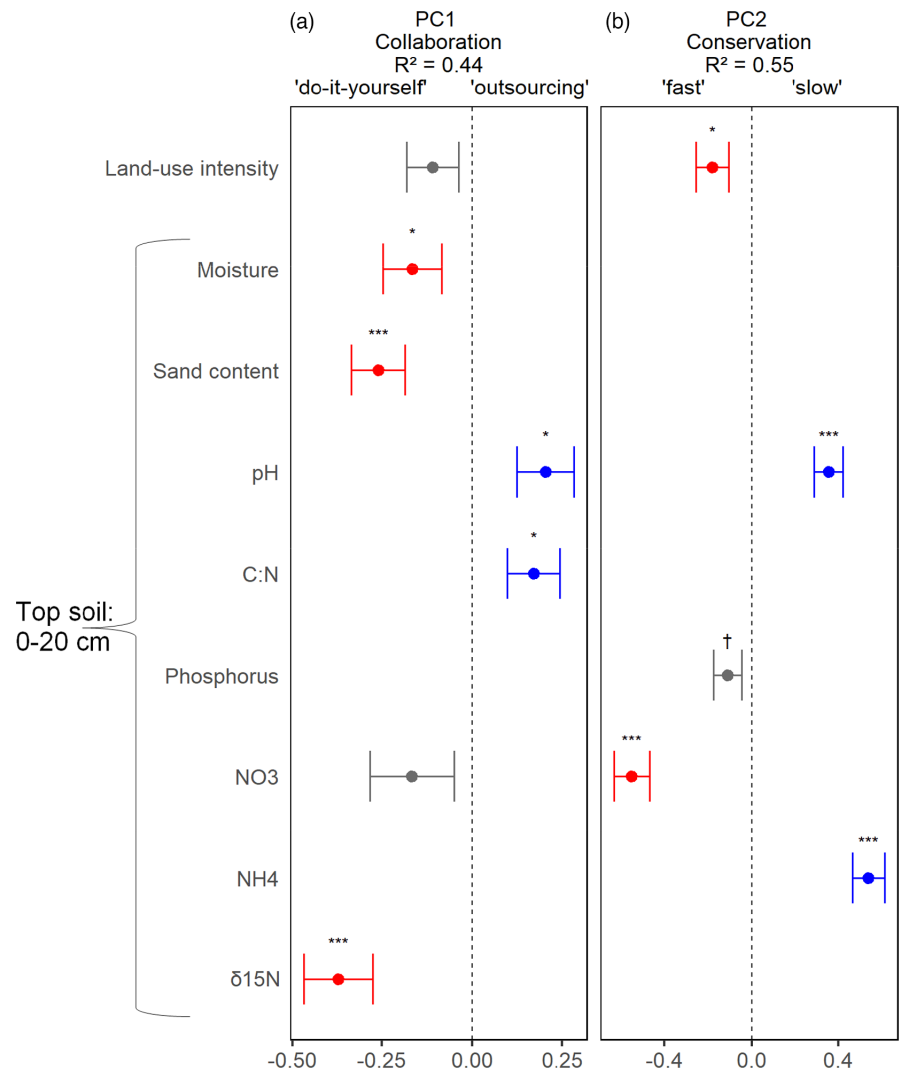
4 | DISCUSSION

We investigated the below-ground trait dimensionality of grassland plant communities and found that a ‘collaboration’ (do-it-yourself vs. outsourcing) and a ‘conservation’ (slow vs. fast) gradient (sensu Bergmann et al., 2020) explained most of the trait variation. Three traits that had not been considered previously in the below-ground trait space were largely belonging to these two dimensions. Namely, $CWM_{Rooting\ depth\ 50\%}$ was associated with the ‘outsourcing’ and ‘fast’ strategies, $CWM_{Branching\ intensity}$ with the ‘do-it-yourself’ strategy, and $CWM_{Bud-bank\ size}$ with the ‘slow’ strategy. Surprisingly, $CWM_{Fine\ roots\ \%N}$ was associated with the ‘outsourcing’ strategy. Both gradients responded to environmental variables related to soil conditions, and fertile soils were generally associated with the ‘fast’ and the ‘do-it-yourself’ strategies.

4.1 | Trait relationships and dimensionality of below-ground traits

Variation in CWMs of below-ground traits separated along two dimensions that largely corresponded to the two ecological root-trait gradients recently identified for variation among species. PC1 related to the collaboration of plants with mycorrhizal fungi. This ‘collaboration’ gradient (sensu Bergmann et al., 2020) ranged from ‘outsourcing’ communities with high mycorrhizal colonization rate and thick roots, but surprisingly also with high root nitrogen content, to ‘do-it-yourself’ communities with high specific root length and root-branching intensity. PC2 corresponded with the construction cost of roots and leaves, and the vegetative regeneration potential. This ‘conservation’ gradient (sensu Bergmann et al., 2020) ranged from ‘slow’ communities with high root tissue density, high root weight ratio and large bud-bank size to ‘fast’ communities with high specific leaf area. Rooting depth related to both PCs, with deep-rooting communities being ‘outsourcing’ and ‘fast’. Also, many of the other traits associated with both PCs (Appendix S9), and consequently the ‘fast’ strategy and ‘do-it-yourself’ strategy partly coincided. This is in

FIGURE 3 Estimates from linear models testing the effects of environmental variables on PCA scores for (a) PC1—'collaboration' gradient and (b) PC2—'conservation' gradient from the Above-Below-ground PCA on community weighted means of traits. On the y-axis are the nine environmental variables that were retained in the most parsimonious models (region and N:P were not retained). The error bars around the estimates depict standard errors. Significant (* for $p < 0.05$; ** for $p < 0.01$; *** for $p < 0.001$) negative and positive estimates are marked in red and blue respectively. Non-significant ($p > 0.05$) estimates are marked in grey. Marginally significant ($0.05 \leq p < 0.10$) estimates are marked with †



accordance with recent global analysis by Laughlin et al. (2021) who found that cold climates enhance the probability of occurrence of 'fast' and 'do-it-yourself' plant species.

Many species traits are phylogenetically conserved (Felsenstein, 1985) and this might also be reflected in the trait dimensions revealed by the CWMs. Indeed, the three plant functional types we considered, and which largely reflect different systematic groups (i.e. Poales, Fabaceae, non-N-fixing dicotyledons), contributed largely to the two main plant-strategy gradients. Communities with a high proportion of Poales were typical of 'do-it-yourself' strategy; communities with a high proportion of Fabaceae represented 'outsourcing' and 'fast' strategy, and communities with a high proportion of non-N-fixing forbs were typically 'outsourcing' and 'slow' (Appendix S6). The trait clustering we found for CWMs was generally in accordance with previous findings of trait clustering among species, both for trees and herbaceous plants (Bergmann et al., 2020; Kramer-Walter et al., 2016; Weemstra et al., 2016). The main exception was $_{CWM} \text{Fine roots \%N}$, which in our study associated with the 'outsourcing' side of the collaboration gradient instead of with the 'fast' side of the conservation gradient. This might be particular to our study using CWMs, because when we did the PCA at the species

level, root N content related to the 'fast' as well as to the 'outsourcing' strategy (Appendix S14). Trait-performance relationships have already been shown to differ between common garden and field conditions in the grasslands included in our study (Breitschwerdt et al., 2019). Notably, the dominance of grasses, which are known to have lower root N than other plant functional types, might drive this pattern (e.g. Tjoelker et al., 2005). The differences in relationships among species traits and among CWMs of traits could also reflect the multiple constraints exerted by environmental filtering and competition on the trait values selected in a field context, which could result in traits relationships that reflect the realized niches of species.

We found that communities with large bud banks were on the 'slow' side of the 'conservation' gradient. Previously, bud-bank size was shown to be rather independent of the plant economics spectrum, as specific leaf area—a key trait in this spectrum—explained less than 2% of variation in bud-bank size among 1359 herbaceous species (Klimešová et al., 2016). In our study, the correlation between species mean values of bud-bank size and specific leaf area was significantly negative (-0.17 , $p < 0.01$; Appendix S14b), though still weaker than between the corresponding CWMs (-0.34 ; Appendix

S9). Because all of our species were selected based on their presence in permanent grasslands, it could be that the association between bud-bank size and 'conservation' traits is a feature of this specific habitat. A smaller bud-bank size was also observed in communities with a 'fast' strategy, typical of resource-rich grasslands, where competition for light might be more intense (Hautier et al., 2009). This could indicate that 'fast' plants invest more in immediate above-ground light-harvesting structures at the cost of resprouting ability. In line with this, we also found that low root weight ratios are indicative of 'fast' communities.

Although we focussed on PC1 and PC2, which together explained ~56% of the variation in CWMs, PC3 explained an additional ~15% of the variation. The strongest loading on PC3 had $CWM_{Rooting\ depth\ 50\%}$ (-0.7), which might suggest the existence of a third below-ground plant-strategy gradient related to size as suggested by Weigelt et al. (2021). However, variation in PC3, as well as in $CWM_{Rooting\ depth\ 50\%}$, was mainly explained by differences between the three regions (Appendices S11 and S14). This pattern most likely reflects that the regions Hainich and Schorfheide have significantly deeper soils, which might facilitate deep-rooting species, than the Alb region (Appendix S2).

The below-ground traits we included in the dimensionality analysis indicated the preponderance of a two-dimensional trait space. It is thought that plant-trait space does not exceed six dimensions (Laughlin, 2014) and that different plant organs might represent different dimensions. Our finding that specific leaf area is part of the 'conservation' gradient points towards the possibility of an integration of traits across multiple organs (Reich, 2014; Weigelt et al., 2021). Similarly, seed mass has also been related to 'outsourcing' traits such as root diameter (Bergmann et al., 2017), and plant height tends to be related to 'slow' traits (Díaz et al., 2016) and to rooting depth at the global scale (Schenk & Jackson, 2002a). All these results suggest that there is a certain degree of integration between traits of different organs.

4.2 | Variation in community trait dimensions explained by the environment

About half of the variation in the 'collaboration' and 'conservation' gradients revealed by our PCAs was explained by environmental variables. Along the 'collaboration' gradient, the 'do-it-yourself' strategy was found on moist, moderately acidic soils with high sand content and intense N cycling (i.e. low C:N-ratio, high $\delta^{15}N$ and marginally high NO_3), and tended to be associated with a high land-use intensity (although not significantly). Along the 'conservation' gradient, the 'fast' strategy was found on moderately acidic soils with high P and NO_3 but low NH_4 availabilities, and in sites with high land-use intensities. Hence, although the 'do-it-yourself' and 'fast' strategies belong to two different plant-strategy gradients, they both tend to be associated with fertile, intensively used sites, while the 'outsourcing' and 'slow' strategies are associated with infertile sites of low land-use intensity. In fact, all plots in the upper right section of

the PCA diagram (Figure 2) originate from calcareous grasslands on shallow, infertile Rendzic Leptosols, which are often used as unfertilized sheep pastures and characterized by P or NP limitation (Klaus et al., 2011). Our results are thus largely in agreement with those of Fort and Freschet (2020) who concluded from a global meta-analysis that herbaceous species with fine root traits typical of fast resource-use strategies tend to occur in more productive soil environments.

The relationships we encountered between the 'collaboration' gradient and environmental variables are generally in accordance with current ecological knowledge. Numerous studies have demonstrated that mycorrhiza have a positive effect on plant growth under water-limited and nutrient-poor conditions (Augé, 2001). In addition, we found that dry habitats are associated with deep-rooting communities (Appendix S12), most likely because they have access to water in deeper soil layers (Fan et al., 2017). Moreover, our results show that 'outsourcing' communities occur on soils with low $\delta^{15}N$ isotopic ratios, which are related to nitrogen origin and cycling (Robinson, 2001). It has been shown for our grassland plots that a low $\delta^{15}N$ is linked to lower above-ground productivity and higher plant species richness (Kleinebecker et al., 2014). So, if we interpret $\delta^{15}N$ as an indicator of plant-available nitrogen, the negative relationship between $\delta^{15}N$ and the 'outsourcing' strategy is in line with the finding of reduced mycorrhizal colonization in response to nitrogen addition (Ma et al., 2020) and with our finding that 'outsourcing' communities tend to be on the 'slow' side of the 'conservation' gradient.

Although arbuscular mycorrhizal fungi are well known to help plants with the uptake of P, we did not find a link between soil plant-available P content and the 'collaboration' gradient (or mycorrhizal colonization; Appendix S12). This could partly be a consequence of the availability of N, as N addition generally decreases the degree of mycorrhizal colonization in conditions of high P availability (as in the study area) and increases it under low P availability (Ma et al., 2020). Indeed, $CWM_{Mycorrhizal\ colonization}$ was marginally significantly associated with the soil N:P ratio (Appendix S12), although there was no association between the 'collaboration' gradient and the N:P ratio. As arbuscular mycorrhizal fungi also help plants with the uptake of N, it could be that the large variation in N availability among plots overrides the effect of P availability. Moreover, the nature of plant-available P in soil is still debated (Barrow, 2021), and P is more available in moderately acidic soils (Alt et al., 2011). In line with this, 'outsourcing' communities with high degrees of mycorrhization were more likely to occur on non-acidic soils.

High land-use intensity and lower soil pH with high P and NO_3 levels were associated with the 'fast' strategy, which is in line with expectations on how soil fertility should relate to the plant economic spectrum. The decrease in bud-bank size at higher soil fertility (Figure 3, Appendix S12) is congruent with recent findings that land-use intensity and N addition decrease total bud density and rhizome biomass in temperate perennial grasslands (Ottaviani et al., 2021; Qian et al., 2021). In contrast to the negative effect of soil NO_3 on the 'conservation' gradient, we found a positive association with soil NH_4 . It has also been shown that there might

be a trade-off between NO_3 and NH_4 uptake in grassland species (Boudsocq et al., 2012). In conclusion, in our study, the form of N available in the soil has contrasting effects on below-ground traits, with NH_4 being more related to the 'slow' strategy and NO_3 more related to the 'fast' strategy.

5 | CONCLUSIONS

The dimensionality of trait syndromes and their relation to environmental variables are of central interest in ecology. Previous studies using species trait values showed that root tissue density, root nitrogen content, root diameter and specific root length form a two-dimensional 'collaboration' and 'conservation' trait space. Here, we largely confirmed this concept using CWMs across a large variety of agricultural grasslands. Moreover, we showed that the traits root-branching intensity, root weight ratio, bud-bank size and rooting depth can also be integrated within this trait space. The variation of both gradients with environmental variables was partly overlapping and partly unique, while indicators of high soil fertility were generally associated with both the 'fast' and the 'do-it-yourself' strategy. Thus, our study clearly shows that the below-ground plant-strategy gradients identified among species are also applicable to plant communities and can be linked to environmental conditions.

ACKNOWLEDGEMENTS

We thank Otmar Ficht, Maximilian Fuchs and Heinz Vahlenkamp for help setting up the experiments, Beate Rüter, Ekaterina Mamonova, Huy Manh Nguyen, Simon Gommel, Maximilian Rometsch, Anika Schick and Emma Bretherick for help measuring the plant traits. We also thank the managers of the three Biodiversity Exploratories, Konstanz Wells, Swen Renner, Kirsten Reichel-Jung, Sonja Gockel, Kerstin Wiesner, Katrin Lorenzen, Andreas Hemp, Martin Gorke and Miriam Teuscher, and all former managers for their work in maintaining the plot and project infrastructure; Christiane Fischer for giving support through the central office, Andreas Ostrowski for managing the central database, and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. The work has been (partly) funded by the DFG Priority Program 1374 'Infrastructure-Biodiversity-Exploratories'. Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen and Brandenburg. We acknowledge funding from the German Research Foundation (DFG, grants KL 1866/12-1 to M.v.K. and 323522591 to M.R.).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

T.L. performed three of the experiments, ran the analyses and wrote the paper; J.B. performed one experiment and participated in one

of the other three; M.R. contributed to the design of the experiments; N.H., V.H.K. and T.K. collected environmental data; M.v.K. designed three of the experiments, advised on data analysis and extensively revised the paper. All authors contributed to revisions of the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13862>.

DATA AVAILABILITY STATEMENT

The data are openly accessible in Dryad Digital Repository (Lachaise, Bergmann, Hölzel, et al., 2021), licensed under a CC0 1.0 Universal (CC0 1.0) Public Domain Dedication licence: <https://doi.org/10.5061/dryad.dfn2z3538>.

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REFERENCES

- Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Blüthgen, N., Böhm, S., Grassein, F., Hölzel, N., Klaus, V. H., Kleinebecker, T., Morris, E. K., Oelmann, Y., Prati, D., Renner, S. C., Rillig, M. C., Schaefer, M., Schloter, M., Schmitt, B., ... Fischer, M. (2015). Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecology Letters*, 18(8), 834–843. <https://doi.org/10.1111/ele.12469>
- Alt, F., Oelmann, Y., Herold, N., Schrupf, M., & Wilcke, W. (2011). Phosphorus partitioning in grassland and forest soils of Germany as related to land-use type, management intensity, and land use-related pH. *Journal of Plant Nutrition and Soil Science*, 174(2), 195–209. <https://doi.org/10.1002/jpln.201000142>
- Augé, R. M. (2001). Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza*, 1(11), 3–42.
- Barrow, N. J. (2021). Comparing two theories about the nature of soil phosphate. *European Journal of Soil Science*, 72(2), 679–685. <https://doi.org/10.1111/ejss.13027>
- Bergmann, J., Ryo, M., Prati, D., Hempel, S., & Rillig, M. C. (2017). Root traits are more than analogues of leaf traits: The case for diaspore mass. *New Phytologist*, 216(4), 1130–1139. <https://doi.org/10.1111/nph.14748>
- Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D. C., Kuyper, T. W., Guerrero-Ramirez, N., Valverde-Barrantes, O. J., Bruelheide, H., Freschet, G. T., Iversen, C. M., Kattge, J., McCormack, M., Meier, I. C., Rillig, M. C., Roumet, C., Semchenko, M., Sweeney, C. J., van Ruijven, J., York, L. M., & Mommer, L. (2020). The fungal collaboration gradient dominates the root economics space in plants. *Science Advances*, 6(27), eaba3756. <https://doi.org/10.1126/sciadv.aba3756>
- Bloom, A. J., Chapin, F. S., & Mooney, H. A. (1985). Resource limitation in plants—An economic analogy. *Annual Review of Ecology and Systematics*, 16, 363–392.
- Blüthgen, N., Dormann, C. F., Prati, D., Klaus, V. H., Kleinebecker, T., Hölzel, N., Alt, F., Boch, S., Gockel, S., Hemp, A., Müller, J.,

- Nieschulze, J., Renner, S. C., Schöning, I., Schumacher, U., Socher, S. A., Wells, K., Birkhofer, K., Buscot, F., ... Weisser, W. W. (2012). A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic and Applied Ecology*, 13(3), 207–220. <https://doi.org/10.1016/j.baee.2012.04.001>
- Boudsocq, S., Niboyet, A., Lata, J. C., Raynaud, X., Loeuille, N., Mathieu, J., Blouin, M., Abbadie, L., & Barot, S. (2012). Plant preference for ammonium versus nitrate: A neglected determinant of ecosystem functioning? *The American naturalist*, 180(1), 60–69. <https://doi.org/10.1086/665997>
- Breitschwerdt, E., Jandt, U., & Bruehlheide, H. (2019). Trait-performance relationships of grassland plant species differ between common garden and field conditions. *Ecology and Evolution*, 9(4), 1691–1701. <https://doi.org/10.1002/ece3.4818>
- Busch, V., Klaus, V. H., Schäfer, D., Prati, D., Boch, S., Müller, J., Chisté, M., Mody, K., Blüthgen, N., Fischer, M., Hölzel, N., & Kleinebecker, T. (2019). Will I stay or will I go? Plant species-specific response and tolerance to high land-use intensity in temperate grassland ecosystems. *Journal of Vegetation Science*, 30(4), 674–686. <https://doi.org/10.1111/jvs.12749>
- Cayuela, L., La Granzow-de Cerda, Í., Albuquerque, F. S., & Golicher, D. J. (2012). Taxonstand: An R package for species names standardisation in vegetation databases. *Methods in Ecology and Evolution*, 3(6), 1078–1083. <https://doi.org/10.1111/j.2041-210X.2012.00232.x>
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12(4), 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Craine, J. M., Froehle, J., Tilman, D. G., Wedin, D. A., & Chapin, I. F. S. (2001). The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos*, 93(2), 274–285. <https://doi.org/10.1034/j.1600-0706.2001.930210.x>
- de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., Berg, M. P., Cipriotti, P., Feld, C. K., Hering, D., Martins da Silva, P., Potts, S. G., Sandin, L., Sousa, J. P., Storkey, J., Wardle, D. A., & Harrison, P. A. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, 19(10), 2873–2893. <https://doi.org/10.1007/s10531-010-9850-9>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529(7585), 167–171. <https://doi.org/10.1038/nature16489>
- Ding, J., Kong, D., Zhang, X., Cai, Q., Xiao, J., Liu, Q., & Yin, H. (2020). Climate and soil nutrients differentially drive multidimensional fine root traits in ectomycorrhizal-dominated alpine coniferous forests. *Journal of Ecology*, 108, 2544–2556. <https://doi.org/10.1111/1365-2745.13407>
- Erktan, A., Roumet, C., Bouchet, D., Stokes, A., Pailler, F., & Munoz, F. (2018). Two dimensions define the variation of fine root traits across plant communities under the joint influence of ecological succession and annual mowing. *Journal of Ecology*, 106(5), 2031–2042. <https://doi.org/10.1111/1365-2745.12953>
- E-Vojtkó, A., Freitag, M., Bricca, A., Martello, F., Compañ, J. M., Küttim M., Kun, R., de Bello, F., Klimešová, J., & Götzenberger, L. (2017). Clonal vs leaf-height-seed (LHS) traits: Which are filtered more strongly across habitats? *Folia Geobotanica*, 52(3), 269–281. <https://doi.org/10.1007/s12224-017-9292-1>
- Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., & Otero-Casal, C. (2017). Hydrologic regulation of plant rooting depth. *Proceedings of the National Academy of Sciences of the United States of America*, 114(40), 10572–10577. <https://doi.org/10.1073/pnas.1712381114>
- Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, 125(1), 1–15.
- Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E. K. V., Linsenmair, K. E., Schulze, E. D., & Weisser, W. W. (2010). Implementing large-scale and long-term functional biodiversity research: The biodiversity Exploratories. *Basic and Applied Ecology*, 11(6), 473–485. <https://doi.org/10.1016/j.baee.2010.07.009>
- Fort, F., & Freschet, G. T. (2020). Plant ecological indicator values as predictors of fine-root trait variations. *Journal of Ecology*, 108(4), 1565–1577. <https://doi.org/10.1111/1365-2745.13368>
- Freschet, G. T., Roumet, C., Comas, L. H., Weemstra, M., Bengough, A. G., Rewald, B., Bardgett, R. D., de Deyn, G. B., Johnson, D., Klimešová, J., Lukac, M., McCormack, M., Meier, I. C., Pagès, L., Poorter, H., Prieto, I., Wurzbürger, N., Zadworny, M., Bagniewska-Zadworna, A., ... Stokes, A. (2020). Root traits as drivers of plant and ecosystem functioning: Current understanding, pitfalls and future research needs. *New Phytologist*, 232, 1123–1158. <https://doi.org/10.1111/nph.17072>
- Garnier, E., Lavorel, S., Ansqer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., ... Zarovali, M. P. (2007). Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, 99(5), 967–985. <https://doi.org/10.1093/aob/mcl215>
- Garnier, E., Navas, M.-L., & Grigulis, K. (2016). Gradients, response traits, and ecological strategies. In E. Garnier, M.-L. Navas, & K. Grigulis (Eds.), *Plant functional diversity. Organism traits, community structure, and ecosystem properties*. Oxford University Press.
- Güsewell, S. (2004). N:P ratios in terrestrial plants: Variation and functional significance. *New Phytologist*, 164(2), 243–266. <https://doi.org/10.1111/j.1469-8137.2004.01192.x>
- Hansch, M., Schweiger, O., Cord, A. F., Volk, M., & Knapp, S. (2020). Plant functional traits shape multiple ecosystem services, their trade-offs and synergies in grasslands. *Journal of Applied Ecology*, 57, 1535–1550. <https://doi.org/10.1111/1365-2664.13644>
- Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, 324(5927), 636–638. <https://doi.org/10.1126/science.1169640>
- Klaus, V. H., Kleinebecker, T., Hölzel, N., Blüthgen, N., Boch, S., Müller, J., Socher, S. A., Prati, D., & Fischer, M. (2011). Nutrient concentrations and fibre contents of plant community biomass reflect species richness patterns along a broad range of land-use intensities among agricultural grasslands. *Perspectives in Plant Ecology, Evolution and Systematics*, 13(4), 287–295. <https://doi.org/10.1016/j.ppees.2011.07.001>
- Kleinebecker, T., Hölzel, N., Prati, D., Schmitt, B., Fischer, M., & Klaus, V. H. (2014). Evidence from the real world: 15 N natural abundances reveal enhanced nitrogen use at high plant diversity in central European grasslands. *Journal of Ecology*, 102(2), 456–465. <https://doi.org/10.1111/1365-2745.12202>
- Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J. M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., ... Peco, B. (2008). The LEDA Traitbase: A database of life-history traits of the northwest European flora. *Journal of Ecology*, 96(6), 1266–1274. <https://doi.org/10.1111/j.1365-2745.2008.01430.x>
- Klimešová, J., Danihelka, J., Chrtěk, J., de Bello, F., & Herben, T. (2017). CLO-PLA: A database of clonal and bud-bank traits of the central European flora. *Ecology*, 98(4), 1179. <https://doi.org/10.1002/ecy.1745>

- Klimešová, J., Martínková, J., & Herben, T. (2018). Horizontal growth: An overlooked dimension in plant trait space. *Perspectives in Plant Ecology, Evolution and Systematics*, 32, 18–21. <https://doi.org/10.1016/j.ppees.2018.02.002>
- Klimešová, J., Martínková, J., & Ottaviani, G. (2018). Belowground plant functional ecology: Towards an integrated perspective. *Functional Ecology*, 32(9), 2115–2126. <https://doi.org/10.1111/1365-2435.13145>
- Klimešová, J., Tackenberg, O., & Herben, T. (2016). Herbs are different: Clonal and bud bank traits can matter more than leaf–height–seed traits. *New Phytologist*, 210(1), 13–17. <https://doi.org/10.1111/nph.13788>
- Kong, D., Ma, C., Zhang, Q., Li, L., Chen, X., Zeng, H., & Guo, D. (2014). Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist*, 203(3), 863–872. <https://doi.org/10.1111/nph.12842>
- Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J., & Laughlin, D. C. (2016). Root traits are multi-dimensional: Specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology*, 104(5), 1299–1310. <https://doi.org/10.1111/1365-2745.12562>
- Lachaise, T., Bergmann, J., Hölzel, N., Klaus, V., Kleinebecker, T., Rillig, M., & van Kleunen, M. (2021). Data from: Soil conditions drive belowground trait space in temperate agricultural grasslands. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.dfn2z3538>
- Lachaise, T., Bergmann, J., Rillig, M. C., & van Kleunen, M. (2021). Below- and aboveground traits explain local abundance, and regional, continental and global occurrence frequencies of grassland plants. *Oikos*, 130, 110–120. <https://doi.org/10.1111/oik.07874>
- Laliberté, E. (2017). Below-ground frontiers in trait-based plant ecology. *New Phytologist*, 213(4), 1597–1603. <https://doi.org/10.1111/nph.14247>
- Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, 102(1), 186–193. <https://doi.org/10.1111/1365-2745.12187>
- Laughlin, D. C., Mommer, L., Sabatini, F. M., Bruelheide, H., Kuyper, T. W., McCormack, M. L., Bergmann, J., Freschet, G. T., Guerrero-Ramírez, N. R., Iversen, C. M., Kattge, J., Meier, I. C., Poorter, H., Roumet, C., Semchenko, M., Sweeney, C. J., Valverde-Barrantes, O. J., van der Plas, F., van Ruijven, J., ... Weigelt, A. (2021). Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. *Nature Ecology & Evolution*, 5, 1–12. <https://doi.org/10.1038/s41559-021-01471-7>
- Ma, X., Geng, Q., Zhang, H., Bian, C., Chen, H. Y., Jiang, D., & Xu, X. (2020). Global negative effects of nutrient enrichment on arbuscular mycorrhizal fungi, plant diversity and ecosystem multi-functionality. *New Phytologist*, 229, 2957–2969. <https://doi.org/10.1111/nph.17077>
- Maire, V., Gross, N., Da Silveira Pontes, L., Picon-Cochard, C., & Soussana, J.-F. (2009). Trade-off between root nitrogen acquisition and shoot nitrogen utilization across 13 co-occurring pasture grass species. *Functional Ecology*, 23(4), 668–679. <https://doi.org/10.1111/j.1365-2435.2009.01557.x>
- McCarthy, M. C., & Enquist, B. J. (2007). Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology*, 21(4), 713–720. <https://doi.org/10.1111/j.1365-2435.2007.01276.x>
- McGonigle, T. P., Miller, M. H., Evans, D. G., Fairchild, G. L., & Swan, J. A. (1990). A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytologist*, 115(3), 495–501. <https://doi.org/10.1111/j.1469-8137.1990.tb00476.x>
- Mommer, L., Van Ruijven, J., de De Caluwe, H., Smit-Tiekstra, A. E., Wagemaker, C. A. M., Joop Ouborg, N., Bögemann, G. M., Van Der Weerden, G. M., Berendse, F., & De Kroon, H. (2010). Unveiling below-ground species abundance in a biodiversity experiment: A test of vertical niche differentiation among grassland species. *Journal of Ecology*, 98(5), 1117–1127. <https://doi.org/10.1111/j.1365-2745.2010.01702.x>
- Mueller, K. E., Tilman, D., Fornara, D. A., & Hobbie, S. E. (2013). Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. *Ecology*, 94(4), 787–793. <https://doi.org/10.1890/12-1399.1>
- Ottaviani, G., Lubbe, F. C., Lepš, J., Lisner, A., Martínková, J., Mudrák, O., & Klimešová, J. (2021). Strong impact of management regimes on rhizome biomass across Central European temperate grasslands. *Ecological Applications*, 31(4), e2317. <https://doi.org/10.1002/eap.2317>
- Ottaviani, G., Molina-Venegas, R., Charles-Dominique, T., Chelli, S., Campetella, G., Canullo, R., & Klimešová, J. (2020). The neglected belowground dimension of plant dominance. *Trends in Ecology & Evolution*, 35(9), 763–766. <https://doi.org/10.1016/j.tree.2020.06.006>
- Pierce, S., Brusa, G., Vagge, I., & Cerabolini, B. E. L. (2013). Allocating CSR plant functional types: The use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Functional Ecology*, 27(4), 1002–1010. <https://doi.org/10.1111/1365-2435.12095>
- Pornon, A., Escaravage, N., & Lamaze, T. (2007). Complementarity in mineral nitrogen use among dominant plant species in a subalpine community. *American Journal of Botany*, 94(11), 1778–1785. <https://doi.org/10.3732/ajb.94.11.1778>
- Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J. H., Maeght, J. L., Mao, Z., Pierret, A., Portillo, N., Rouspard, O., Thammahacksa, C., & Stokes, A. (2015). Root functional parameters along a land-use gradient: Evidence of a community-level economics spectrum. *Journal of Ecology*, 103(2), 361–373. <https://doi.org/10.1111/1365-2745.12351>
- Qian, J., Wang, Z., Klimešová, J., Lü, X., & Zhang, C. (2021). Belowground bud bank and its relationship with aboveground vegetation under watering and nitrogen addition in temperate semiarid steppe. *Ecological Indicators*, 125, 107520. <https://doi.org/10.1016/j.ecolind.2021.107520>
- R Core Team. (2020). *R: A language and environment for statistical computing*. Retrieved from <https://www.R-project.org/>
- Reich, P. B. (2014). The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Reynolds, H. L., & D’Antonio, C. (1996). The ecological significance of plasticity in root weight ratio in response to nitrogen: Opinion. *Plant and Soil*, 185(1), 75–97. <https://doi.org/10.1007/BF02257566>
- Robinson, D. (2001). $\delta^{15}\text{N}$ as an integrator of the nitrogen cycle. *Trends in Ecology & Evolution*, 16(3), 153–162. [https://doi.org/10.1016/S0169-5347\(00\)02098-X](https://doi.org/10.1016/S0169-5347(00)02098-X)
- Roddy, A. B., Martínez-Perez, C., Teixido, A. L., Cornelissen, T. G., Olson, M. E., Oliveira, R. S., & Silveira, F. A. O. (2020). Towards the flower economics spectrum. *New Phytologist*, 229(2), 665–672. <https://doi.org/10.1111/nph.16823>
- Schachtschabel, P., Blume, H.-P., Brümmer, G., Hartge, K.-H., & Schwertmann, U. (1998). *Lehrbuch der Bodenkunde* (14th ed.). Enke Verlag Stuttgart.
- Schenk, H. J., & Jackson, R. B. (2002a). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, 90(3), 480–494.
- Schenk, H. J., & Jackson, R. B. (2002b). The global biogeography of roots. *Ecological Monographs*, 72(3), 311–328. [https://doi.org/10.1890/0012-9615\(2002\)072\[0311:TGBOR\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072[0311:TGBOR]2.0.CO;2)
- Shipley, B., de Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180(4), 923–931. <https://doi.org/10.1007/s00442-016-3549-x>
- Solbrig, O. T. (1993). Plant traits and adaptive strategies: Their role in ecosystem function. In E.-D. Schulze (Ed.), *Biodiversity and ecosystem function* (pp. 97–116). Springer Berlin Heidelberg.

- Thorup-Kristensen, K., Halberg, N., Nicolaisen, M., Olesen, J. E., Crews, T. E., Hinsinger, P., Kirkegaard, J., Pierret, A., & Dresbøll, D. B. (2020). Digging deeper for agricultural resources, the value of deep rooting. *Trends in Plant Science*, 25(4), 406–417. <https://doi.org/10.1016/j.tplants.2019.12.007>
- Tjoelker, M. G., Craine, J. M., Wedin, D., Reich, P. B., & Tilman, D. (2005). Linking leaf and root trait syndromes among 39 grassland and savannah species. *The New Phytologist*, 167(2), 493–508. <https://doi.org/10.1111/j.1469-8137.2005.01428.x>
- van der Plas, F., Schröder-Georgi, T., Weigelt, A., Barry, K., Meyer, S., Alzate, A., Barnard, R. L., Buchmann, N., de Kroon, H., Ebeling, A., Eisenhauer, N., Engels, C., Fischer, M., Gleixner, G., Hildebrandt, A., Koller-France, E., Leimer, S., Milcu, A., Mommer, L., ... Wirth, C. (2020). Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nature Ecology & Evolution*, 4(12), 1602–1611. <https://doi.org/10.1038/s41559-020-01316-9>
- Weemstra, M., Mommer, L., Visser, E. J. W., van Ruijven, J., Kuyper, T. W., Mohren, G. M. J., & Sterck, F. J. (2016). Towards a multidimensional root trait framework: A tree root review. *New Phytologist*, 211(4), 1159–1169. <https://doi.org/10.1111/nph.14003>
- Weigelt, A., Bol, R., & Bardgett, R. D. (2005). Preferential uptake of soil nitrogen forms by grassland plant species. *Oecologia*, 142(4), 627–635. <https://doi.org/10.1007/s00442-004-1765-2>
- Weigelt, A., Mommer, L., Andrzejak, K., Iversen, C. M., Bergmann, J., Bruelheide, H., Fan, Y., Freschet, G. T., Guerrero-Ramírez, N. R., Kattge, J., Kuyper, T. W., Laughlin, D. C., Meier, I. C., Plas, F., Poorter, H., Roumet, C., Ruijven, J., Sabatini, F. M., Semchenko, M., ... McCormack, M. L. (2021). An integrated framework of plant form and function: The belowground perspective. *New Phytologist*, 232, 42–59. <https://doi.org/10.1111/nph.17590>
- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33(1), 125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. <https://doi.org/10.1038/nature02403>

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How to cite this article: Lachaise, T., Bergmann, J., Hölzel, N., Klaus, V. H., Kleinebecker, T., Rillig, M. C. & van Kleunen, M. (2022). Soil conditions drive below-ground trait space in temperate agricultural grasslands. *Journal of Ecology*, 110, 1189–1200. <https://doi.org/10.1111/1365-2745.13862>