CHAPTER FIVE

Plant functional trait identity and diversity effects on soil meso- and macrofauna in an experimental grassland

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Abstract

Understanding aboveground-belowground linkages and their consequences for ecosystem functioning is a major challenge in soil ecology. It is already well established that soil communities drive essential ecosystem processes, such as nutrient cycling, decomposition, or carbon storage. However, knowledge of how plant diversity affects belowground community structure is limited. Such knowledge can be gained from studying the main plant functional traits that modulate plant community effects on soil fauna. Here, we used a grassland experiment manipulating plant species richness and plant functional diversity to explore the effects of community-level plant traits on soil meso- and macrofauna and the trophic structure of soil fauna by differentiating predators and prey. The functional composition of plant communities was described by six plant traits related to spatial and temporal resource use: plant height, leaf area, rooting depth, root length density, growth start, and flowering start. Community-Weighted Means (CWMs), Functional Dissimilarity (FDis), and Functional Richness (FRic) were calculated for each trait. Community-level plant traits better explained variability in soil fauna than did plant species richness. Notably, each soil fauna group was affected by a unique set of plant traits. Moreover, the identity of plant traits (CWM) explained more variance of soil fauna groups than trait diversity. The abundances of soil fauna at the lower trophic levels were better explained by community-level plant traits than higher trophic levels soil fauna groups. Taken together, our results highlight the importance of the identity of different plant functional traits in driving the diversity and trophic structure of soil food communities.

1. Introduction

Over the past decades, ecologists have extensively studied aboveground-belowground linkages (Bardgett and Wardle, 2010) and their effects on ecosystem properties (Wardle et al., 2004). Plants have been identified as a major ecological link between these compartments (Grime, 2001; Wardle et al., 2004), by providing carbon resources and nutrients to both aboveground and belowground consumer communities (Bardgett and Wardle, 2010) that are connected through feeding relationships with plants (e.g. Johnson et al., 2012; McKenzie et al., 2013). Given these aboveground-belowground interactions, it is not surprising that aboveground and belowground diversity were reported to be positively linked (De Deyn and Van Der Putten, 2005; Scherber et al., 2010).

During the last years, it has been highlighted that changes in plant diversity can have significant consequences for the structure and functioning of above- and belowground consumer communities (Ebeling et al., 2018b; Eisenhauer et al., 2013; Giling et al., 2019; Haddad et al., 2009; Hertzog et al., 2017; Hines et al., 2019; Hooper et al., 2000; Meyer et al., 2017; Schuldt et al., 2019). For aboveground consumer communities, recent studies in experimental grasslands have shown that a loss of plant species causes a reduction in the functional richness and composition of herbivores and omnivores (Ebeling et al., 2018a), as well as a shift in food web structure (Giling et al., 2019). Although plant diversity effects on belowground consumer communities have received less attention, the few existing papers reported a positive relationship between plant diversity and soil microbial biomass (Eisenhauer et al., 2010a,b; Lange et al., 2019; Strecker et al., 2016) as well as between abundance and diversity of soil meso- and macrofauna (Eisenhauer et al., 2011a, 2013; Milcu et al., 2013; Scherber et al., 2010). Identifying the underlying mechanisms of these relationships are subject to current research (e.g. Eisenhauer et al., 2019; Mellado-Vázquez et al., 2016).

In the past decade, considerable progress has been made to identify the mechanisms behind plant diversity effects on ecosystem properties using plant functional traits (Diaz and Cabido, 2001; Flynn et al., 2011; Reich et al., 2012). The significance of plant traits for selected ecosystem functions is now well described (Lavorel and Garnier, 2002; Roscher et al., 2012). For instance, early studies found strong effects of leaf traits on net primary productivity (Violle et al., 2007), litter decomposability (Kazakou et al., 2006), and the species richness of aboveground arthropods (Symstad et al., 2000). More recently, research on soil community responses to plant traits has accelerated (e.g. Eisenhauer and Powell, 2017; Laliberté, 2016; Milcu et al., 2013; Steinauer et al., 2017). These studies have provided evidence that functionally and phylogenetically diverse plant communities enhance the density and diversity of soil fauna (Milcu et al., 2013), and that soil microbial communities and associated functions are mainly driven by plant traits related to spatial resource acquisition (Steinauer et al., 2017). These previous findings were related to effects of dominant plant traits on ecosystem properties. Such dominant plant effects were expressed in the 'biomass ratio hypothesis' by Grime (1998), which predicts that effects of specific plant functional traits on ecosystem properties (e.g. soil biota) should be largely determined by the species dominating the biomass of the plant community (Steinauer et al., 2017). Moreover, those first examples highlight the potential that plant traits have for improving our understanding of plant community effects on soil biota (Eisenhauer and Powell, 2017; Laliberté, 2016).

Despite these findings, understanding the effects of specific above- and belowground plant traits on soil communities remains limited. To address this gap in knowledge, we studied the importance of single plant functional traits related to spatial and temporal resource acquisition on soil meso- and macrofauna in the framework of the so-called Trait-Based Biodiversity Experiment (TBE; Ebeling et al., 2014). This experiment manipulates species richness and functional diversity of plant communities based on spatial- and temporal resource acquisition traits in a crossed factorial design (Ebeling et al., 2014). It is therefore suited to calculate trait diversity (here: Functional Richness and Functional Dispersion; Laliberté et al., 2014; Villéger et al., 2008), and the expression of single plant traits at the community level (here: Community Weighted Mean: CWM, Garnier et al., 2004; Lavorel et al., 2008; Fig. S1 in Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004). We sampled soil fauna communities (7796 individuals from 68 morphospecies) on 138 experimental plots, and we grouped individuals either based on their general size class (soil macrofauna and mesofauna), or feeding strategy (predator and prey). For each of these fauna groups, we quantified the abundance and species richness.

We tested the following hypotheses:

Hypothesis 1. Plant species richness and diversity of plant functional traits will positively affect the abundance and species richness of soil fauna communities. Our hypothesis is based on earlier findings of a positive relationship between plant species richness and soil fauna communities (Eisenhauer et al., 2011a; Milcu et al., 2013). Similarly, the diversity of plant traits might increase the diversity of microenvironments and/or resources (e.g. root traits; Hooper et al., 2000; Kuzyakov and Blagodatskaya, 2015; Postma and Lynch, 2012).

Hypothesis 2. A high community-level expression (i.e. high CWM) and diversity of plant traits related to high root productivity are particularly important for the abundance and diversity of soil fauna communities. This hypothesis is based on previous studies showing significant effects of root inputs (Eisenhauer et al., 2017; Kuzyakov and Blagodatskaya, 2015) and root length density on soil microorganisms (Steinauer et al., 2017), and the CWM root length density and rooting depth, that have been shown to be related to the quantity of carbon inputs to decomposers (Bardgett et al., 2014). Also, this hypothesis is in line with the concept of niche complementarity through different resource foraging strategies (Tilman, 1982, 1988), suggesting that the diversity of habitats and resources in soil (i.e. diversity of plant traits) will facilitate the coexistence of a high number of consumer species (Hooper et al., 2000)

Hypothesis 3. The community-level expression (CWM) and diversity of plant traits related to temporal resource acquisition have a strong effect on shaping soil fauna communities. For example, a plant community containing species differing in their peak growth (i.e. high phenological diversity) might provide resources to the belowground compartment evenly throughout the growing season, thereby supporting diverse soil fauna communities (Kuzyakov and Blagodatskaya, 2015), as well as, increasing community level expression (CWM) of temporal traits may delay species population dynamics in the season. By testing our Hypotheses 2 and 3, we thus sought to identify which community-level plant traits drive soil fauna community composition.

Hypothesis 4. The diversity and expression of certain traits within a plant community have strong effects on consumers at lower trophic levels (herbivores and decomposers), with attenuating bottom-up effects on higher trophic levels (Kaunzinger and Morin, 1998; Scherber et al., 2010). This is in line with a previously shown bottom-up effect of plant diversity on consumers (Eisenhauer et al., 2013; Haddad et al., 2001; Scherber et al., 2010).

2. Material and methods

2.1 Experimental design

This study was conducted in the Trait-Based Biodiversity Experiment (TBE; Ebeling et al., 2014) established in 2010 within the framework of a long-term grassland biodiversity experiment (Jena Experiment, Roscher et al., 2014). The experimental site is located in the floodplain of the Saale river close to the city of Jena (Germany; 50°55′ N, 11°35′ E, 130 m a.s.l.). Mean annual air temperature is 9.9 °C, and mean annual precipitation is 610 mm (1981–2010; Hoffmann et al., 2014) in the region. Before the establishment of the experiment, the area had been an unfertilized mown grassland for 8 years. In 2010, the previous grassland community was removed and new plant communities were sown on 138 plots (3.5 × 3.5 m) to cover a gradient of plant species richness (1, 2, 3, 4, and 8) and plant functional diversity (1, 2, 3, and 4) (see Ebeling et al., 2014).

The functional diversity gradient was formed by the selection of six resource acquisition traits: two aboveground spatial traits [maximum plant height (MH) and leaf area (LA)], two belowground spatial traits [rooting depth (RD) and root length density (RLD)], and two temporal traits [growth start (GS) and flowering start (FS)]. Those traits were analysed by a standardized Principal Component Analysis (PCA) (Ebeling et al., 2014) including all 48 non-legume species of the species pool of the Jena Experiment. The PCA axis 1 spans a gradient of spatial resource acquisition traits, and the PCA axis 2 displays a gradient of temporal resource acquisition traits. The PCA axes were divided into four sectors, and two species from each sector were selected to create three plant species pools each comprising eight species: species pool 1 covers species along the entire axis 1 with an intermediate position on axis 2; species pool 2 covers species along the entire axis 2 with an intermediate position on axis 1; and species pool 3 is the combination of the extremes of both axes (Ebeling et al., 2014). Plant communities were assembled in order to show a gradient in trait dissimilarity between species according to their assignment to different sectors along the two leading axes of the PCA. The experimental plots were arranged in three blocks accounting for variation in soil properties (see Ebeling et al., 2014).

2.1.1 Soil fauna sampling

In September 2014, i.e., 4 years after establishment of the plant communities, soil cores for soil mesofauna (5 cm deep, 5 cm diameter, Macfadyen, 1961) and soil macrofauna (10 cm deep, 25 cm diameter, Kempson et al., 1963) were sampled, taking one sample per plot for each method. Soil arthropods were extracted by a gradual heating, collected in glycol, and then stored in 70% ethanol until identification. For both mesofauna and macrofauna, we only recorded taxonomic groups that were adequately assessed by these extraction methods. For mesofauna samples, we identified mites (Krantz and Walter, 2009) and collembolans (Hopkin, 2007). For macrofauna samples, we separated chilopods, symphylans, diplopods, hemipterans (Aphidoidea), and beetles (Staphylinidae) (Coleman et al., 2004; Table S1 in Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004). Other taxonomic groups were excluded from analyses, because the method of extraction was considered inappropriate (e.g. for Diptera larvae). All extracted fauna from the target taxonomic groups were assigned to morphospecies based on consistent morphological characteristics. They were further assigned to trophic groups by using information from the literature on their respective taxonomic groups (Coleman et al., 2004; Table S1 in Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004). We defined all lower trophic level consumers (i.e. herbivores and decomposers) as ‘prey’, and all higher trophic levels as ‘predators’.

The dataset contained 121 samples for each meso- and macrofauna as some samples were lost during the extraction procedure.

2.1.2 *Plant cover measurement*

Plant-specific cover (%) of sown plant species in each plot was estimated by using a decimal scale (modified after Londo, 1976) on the entire plot area (3.5 × 3.5 m) in mid-August 2014. The realized plant community composition and species relative abundances were used to calculate abundance-weighted plant community indices (see below).

2.2 Plant community indices

Two indices of plant trait diversity were calculated: Functional Richness (FRic) and Functional Dispersion (FDis) (Fig. S1 in Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004). All calculations were performed for each trait separately, which means that the functional diversity indices only refer to one dimension. In one-dimensional space (i.e. one trait), Functional Richness (FRic) is defined as the range between the maximum and minimum of the trait values within the plant community (Villéger et al., 2008), and Functional Dispersion (FDis) is defined as the weighted variance of the trait values within the plant community (Laliberté and Legendre, 2010). These indices have been identified to be more sensitive to processes of community assembly than species richness (Laliberté and Legendre, 2010; Roscher et al., 2014), and they describe trait distributions in two complementary ways: Functional Richness describes the range of trait values within a community, while Functional Dispersion informs on how evenly species trait values are distributed along this range. Further, we calculated CWM of each trait, based on their species-specific cover for each plant community in 2014 (Garnier et al., 2004; Lavorel et al., 2008; Roscher et al., 2012). To avoid differences of too many orders of magnitude between the explanatory variables, they were rescaled based on range to fit between -1 and 1. The calculations were performed with the R package FD (Laliberté et al., 2014).

2.3 Statistical analyses

We used linear mixed-effects models to test the effects of plant species richness on the abundance and species richness of all soil fauna, mesofauna, macrofauna, corresponding subgroups of predators and prey. Species abundance and richness were modelled using a Poisson distribution with observation-level random effects to take in account over-dispersion (Blolker, 2019; Elston et al., 2001). For each model, ‘block’ was specified as a random effect to account for the spatial arrangement of the plots. Linear mixed-effects models were performed using the 'lme4' package (Bates et al., 2012) within the R statistical environment (R Development Core Team, 2010).

To identify the effect of plant trait-based indices on each soil fauna group, we proceeded in two steps: (1) for each index (CWM, FDis, FRic), we selected a subset of important traits, and (2) we built a full trait-based model composed of the traits selected into the subsets of each index (CWM, FDis, and FRic). (1) *Trait selection for each of the three indices describing community-level plant traits (FRic, FDis, and CWM):* we employed a model selection approach following Burnham and Anderson (2002) and Grueber et al. (2011). For a given index, we used linear mixed-effect models to test the effect of the six plant traits (growth start, flowering start, leaf area, maximum height, root length density, and rooting depth) on soil fauna groups. All possible combinations of the six plant traits were modelled for each response variable (abundance and species richness) of each fauna group (total fauna, macrofauna, mesofauna, mesofauna predators, mesofauna prey, macrofauna predators, and macrofauna prey). A set of best candidate models was defined by all models with a maximum ΔAICc of 2 compared to the model with the lowest AICc (Bolker et al., 2009; Burnham and Anderson, 2002). For each response variable, we selected all explanatory variables included in the set of best candidate models (Grueber et al., 2011; Nakagawa and Freckleton, 2011). Trait selection was performed using the R package 'MuMIn' (Barton, 2015). (2) *Trait-based model:* we used linear mixed-effect models to test the effect of all traits previously selected for all indices on each response variable. For both steps and as done in the plant species richness models, species abundances and richness were modelled with a Poisson distribution with observation-level random effects, and 'block' was specified as a random effect. Finally, for each group of soil fauna, we calculated the proportion of total variance explained by the trait-based models using marginal R^2. R^2 were calculated following Nakagawa and Schielzeth (2013).

To compare plant species richness and trait-based models, we compared the AICc of plants species richness-based model predictions (Eq. 1) or trait-based model predictions (Eq. 2) and the AICc of the model with both plants species richness and trait-based model predictions as explanatory variables:

$$\Delta AICc_1 = AICc(y \sim trait.prediction) - AICc(y \sim trait.prediction + PD) \quad (1)$$

$$\Delta AICc_2 = AICc(y \sim PD) - AICc(y \sim PD + trait.prediction) \quad (2)$$

where, *y* is our response variable, *PD* is the plant species richness, and *trait. prediction* is the prediction of the corresponding trait-based model. We considered the models distinct when $|\Delta AICc| > 2$. If $AICc_1 > 2$, adding plant species richness improved our model predictions, while if $AICc_2 > 2$, adding traits indices improved our model predictions.

3. Results

3.1 Plant species richness effects

Plant species richness did not have any significant effect on neither abundance nor species richness of our studied fauna groups (Fig. 1; Supplementary

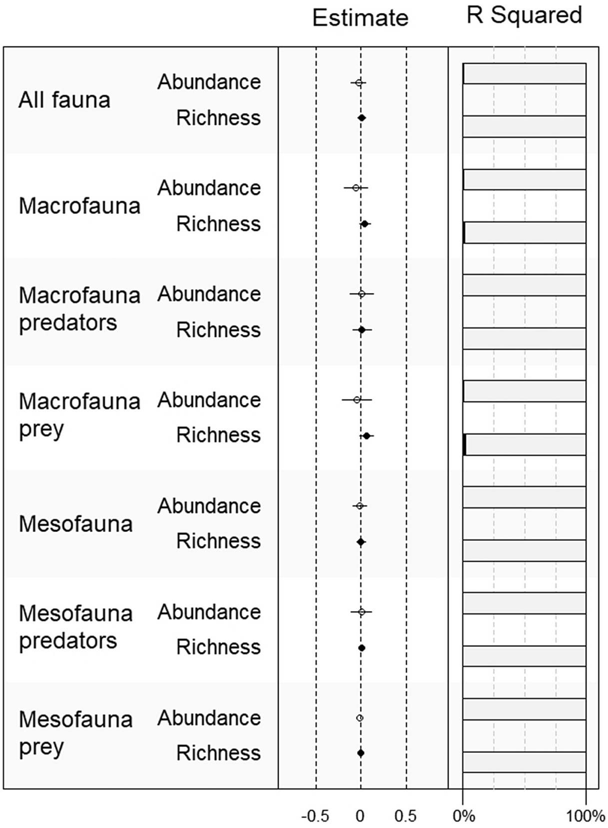

Fig. 1 Plant species richness effects on soil fauna abundance and species richness. Circles indicate the estimates of plant species richness effects on the different indices of soil fauna groups with a confidence interval of 95%.

Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S1). The variance explained by plant species richness in our model was extremely low (from $R^2 < 0.01$ to $R^2 = 0.016$; Fig. 1; Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S1).

3.2 Trait-based models

For each trait index, we selected a subset of the most relevant traits. However, FDis and FRic indices were highly correlated (Pearson's correlation: 0.97 +/− 0.01, Fig. S2 in Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004), and the subsets of traits selected were similar (see Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S2 and S3A). Given these similarities, we only used the traits selected for FDis to build out trait-based models.

For soil fauna abundance, we observed that the amount of variance explained by our trait-based models differed between groups of soil fauna. More specifically, our models explained only a small fraction of all fauna variability ($R^2 = 0.04$; Fig. 2; Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S3B), while size based groups were better explained (macrofauna $R^2 = 0.16$ and mesofauna $R^2 = 0.05$; Fig. 2; Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S3B). Moreover, the abundance of prey was better explained than that of predators for a given size-based group (macrofauna or mesofauna, Fig. 2). A unique set of explanatory variables was selected for each fauna group (Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S3A). For example, both macrofauna and mesofauna abundance models included CWM root length density, maximum height, and growth start, while the model for mesofauna abundance also included CWM flowering start and FDis of all six traits (see Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S3A and Fig. 2).

Overall, our models revealed that CWM indices had a higher explanatory power than FDis indices. None of the FDis indices had a significant effect on any soil fauna group (Fig. 2; Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S3B). Of the CWM indices, two traits had strong effects on soil fauna abundances. First, CWM root length density had a positive effect on macrofauna (estimate = 0.44, *P*-value = 0.04),

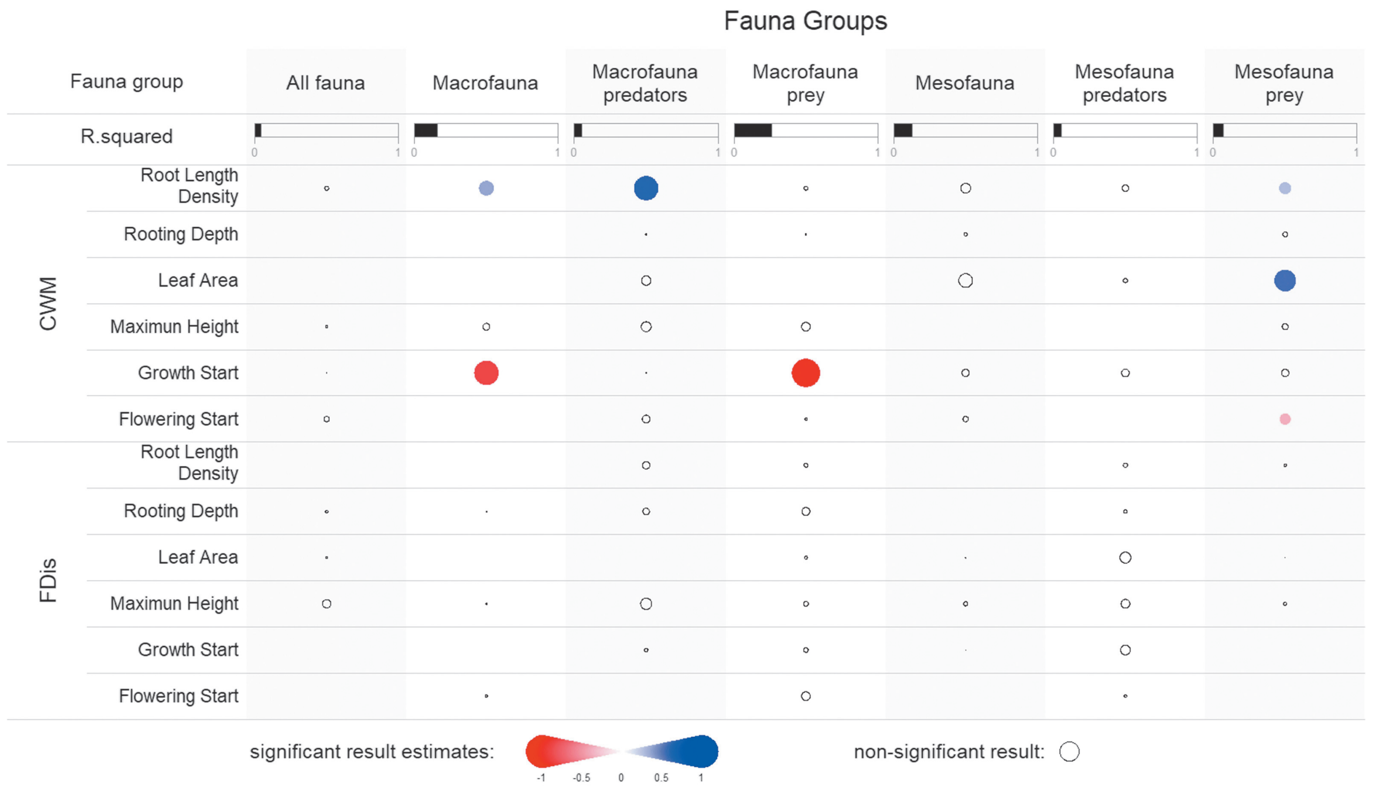

Fig. 2 Plant functional trait effects on soil fauna abundance. Circle size and colour indicate the estimates of a given trait effect on the abundance of soil fauna groups. Blue circles denote positive estimates, red circles denote negative estimates and empty circles denote a non-significant relationship (i.e. *P*-value <0.05).

macrofauna predator species (estimate = 0.74, *P*-value = 0.002), and mesofauna prey (estimate = 0.35, *P*-value = 0.05; Fig. 2; Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S3B). Second, CWM growth start had a strong negative effect on macrofauna (estimate = − 0.74, *P*-value <0.001) and macrofauna prey (estimate = − 0.86, *P*-value = 0.03; Fig. 2; Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S3B). The other traits had more inconsistent and weaker effects across fauna groups (e.g. a positive effect of CWM leaf area on mesofauna prey and negative effect of CWM flowering start on mesofauna prey; Fig. 2). Our models did not show any significant trend for species richness of soil fauna groups, although the explained variance was within the same order of magnitude (Fig. S3 in Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004).

3.3 Comparison of plant species richness-based and trait-based models

For abundance of all fauna groups, adding plant species richness to the plant trait-based models did not improve the model ($\Delta AICc_1 \leq 2$; Fig. 3; Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S4), while adding plant traits to a plant species richness-based model significantly improved the model predictions ($\Delta AICc_2$ from 213 to 45′714; Fig. 3; Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004 S4). These results indicate that variance explained by the plant trait-based model already accounts for the variance explained by plant species richness. By contrast, the plant trait-based model explained a higher proportion of variance than the plant species richness model and was not improved by including plant species richness in the model (Fig. 3). We observed the same for the species richness of soil fauna groups; however, the overall explanatory power of the models was low (Fig. S4 in Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004).

4. Discussion

Our results revealed that plant traits play a significant role in structuring soil communities (Hypothesis 1), whereas plant species richness appeared to be of relatively minor importance in the present study. Importantly, we found that different feeding groups (predator and prey) and size classes

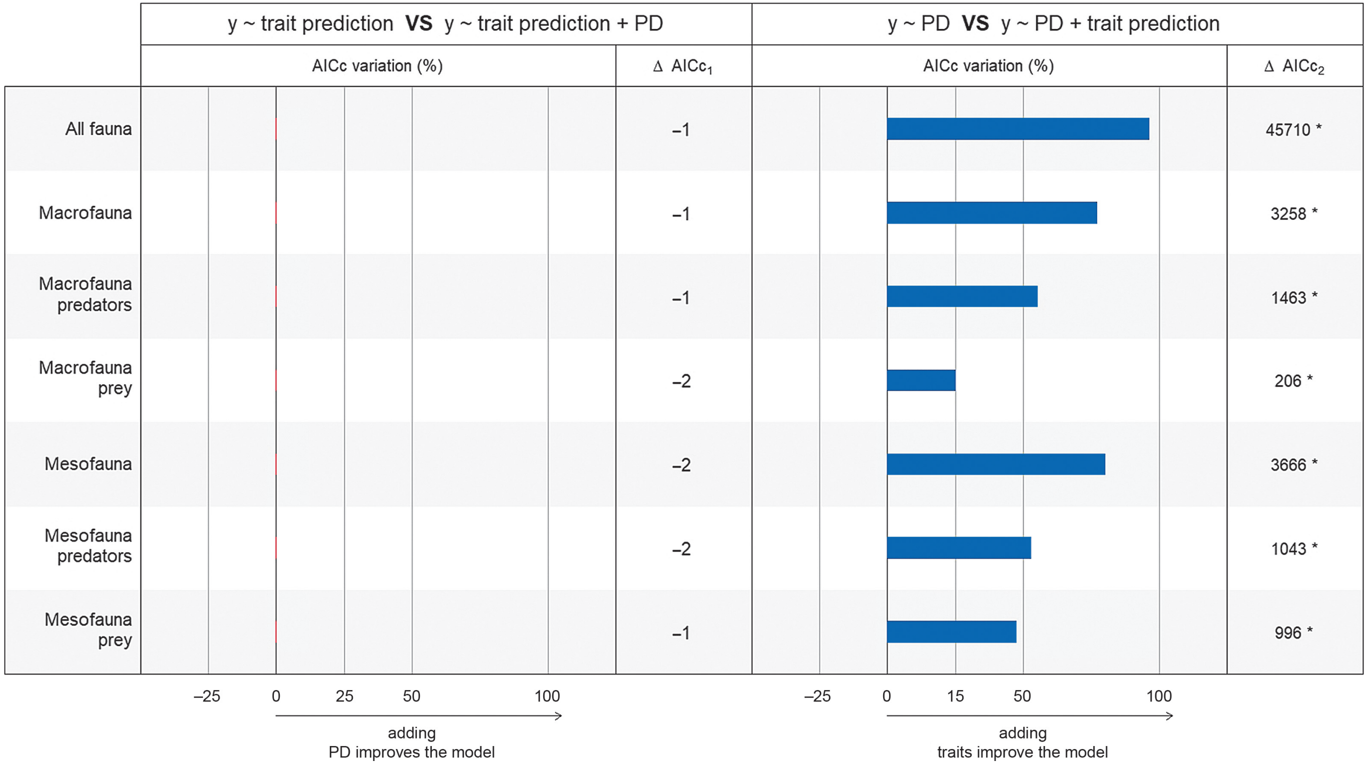

Fig. 3 Comparison between plant species richness-based models and trait-based models explaining abundances of soil fauna groups. For each fauna group, a positive variation of AICc (blue line) and a ΔAICc >2 indicate that the information added to the model (i.e. plant species richness—PD—or trait prediction) increased the model prediction.

(meso- and macrofauna) were affected by different sets of community-level plant traits. Taken together, our results indicate that the expression of certain plant traits at the community level governs the structure of soil fauna communities.

4.1 Plant species richness has a weak effect on soil communities

Surprisingly, we found that plant species richness had no significant effect on the abundance and species richness of any soil fauna group (Fig. 1). These results contradict our Hypothesis 1 and findings from previous studies on both aboveground and belowground communities (e.g. Ebeling et al., 2018a; Eisenhauer et al., 2011; Haddad et al., 2009; Milcu et al., 2013; Scherber et al., 2010; Schuldt et al., 2019) that showed positive plant diversity effects on the abundance and diversity of consumers. Moreover, our results are in contrast to the 'More Individuals Hypothesis', which predicts an increase of plant productivity with increasing plant species richness, and consequently an increase of herbivorous and detritivorous species (Srivastava and Lawton, 1998). Non-significant plant diversity effects on soil fauna have been observed before (e.g. Eisenhauer et al., 2009; Milcu et al., 2008), which is possibly explained by the short-term duration of most previous experiments as plant diversity effects need several years to manifest (Eisenhauer et al., 2010a,b, 2012). This is because plant community-specific organic matter gradually accumulates following the establishment of the experimental grassland plots (Habekost et al., 2008), which in turn drives the assembly of specific soil communities (Eisenhauer et al., 2011b). As a consequence, these results should be treated with care as longer-term studies are required to test plant diversity-ecosystem functioning relationships (Cardinale et al., 2007; Reich et al., 2012; Thakur et al., 2015).

4.2 Plant traits as more powerful predictors of soil fauna communities

Although only a small proportion of the variance of soil fauna groups was explained by plant functional traits (max. 16%), they generally explained more variance than plant species richness. In fact, functional traits have often been argued to underlie significant plant diversity effects (e.g. Milcu et al., 2013; Mouillot et al., 2013). Previous research from the Jena Experiment, however, has shown that long-term effects of plant species richness on soil organisms are more important than plant functional group effects (e.g. Eisenhauer et al., 2010a,b, 2011a). Notably, these previous studies used broad categories of plant functional groups, but did not consider finer gradients in spatial and temporal resource use traits (Ebeling et al., 2014). Moreover, the present study did not include any legumes, which have repeatedly been shown to play a major role for soil communities and processes by fixing nitrogen through their mutualistic relationship with rhizobia (Eisenhauer et al., 2009; Lange et al., 2015; Milcu et al., 2008; Spehn et al., 2000). In addition, it should be noted that species richness of soil fauna was poorly explained by our models, which may be the result of a low variability of species richness within each given fauna group (Table S1 in Supplementary Material in the online version at https://doi.org/10.1016/bs.aecr.2019.06.004).

4.3 The importance of plant trait identity effects across soil fauna groups

We observed that our plant trait-based model varied in its explanatory power for soil fauna abundance depending on the fauna group. While only a small fraction of the variance of all soil fauna was explained by the model ($R^2 = 0.04$), 16% of the variance in soil macrofauna abundance was explained. Moreover, for both macrofauna and mesofauna, explanatory power for prey abundance was always higher than for predators (providing support for our Hypothesis 4). These findings are in line with previously found bottom-up effects of plant community properties on consumer species (see Eisenhauer et al., 2010a,b, 2013; Scherber et al., 2010), whereby the strength of plant community effects decreased with increasing trophic level (Kaunzinger and Morin, 1998; Scherber et al., 2010).

While these results broadly confirm previous findings, our study provides particularly novel insights into how different traits exert significant effects on meso- and macrofauna predators and prey. Thus, our study emphasizes that different facets of plant community traits likely affect soil food web structure (see Schuldt et al., 2019 for aboveground invertebrate food webs) and that some plant community effects on predators may be mediated by variations in their prey populations, while there may be other simultaneous direct effects of vegetation structure. For instance, macrofauna predators were mainly affected by CWM root length density, while macrofauna prey were mainly affected by CWM growth start. In our final plant trait-based model, CWM traits showed stronger effects on soil fauna than plant trait diversity (Fig. 2). These observations suggest that dominant plant trait values are more important than the diversity of plant traits for specific groups of soil fauna. This is in line with the 'biomass ratio hypothesis' (Grime, 1998) that predicts a stronger effect of dominant species within a community. Nevertheless, the finding of dissimilar traits influencing different groups of soil fauna might provide a mechanism underlying the often-observed positive plant diversity effects on soil communities (e.g. Eisenhauer et al., 2013; Scherber et al., 2010).

4.4 Soil fauna responses to spatial resource acquisition traits

Our models highlighted the importance of two spatial resource acquisition traits: root length density and leaf area. These results are in the line with Hypothesis 2—that both CWM and diversity of plant traits related to high root productivity should influence soil community structure—and confirm previous findings for soil microbial communities (Steinauer et al., 2017). Root length density (RLD) affected several fauna groups (Hypothesis 2). In particular, macrofauna predator abundance and mesofauna prey abundance increased with CWM root length density. CWM root length density may be related to an increase of plant-derived carbon inputs to the soil that are available for primary consumers (i.e. herbivores or decomposers; Bardgett et al., 2014). Therefore, we suspect that the effect of CWM root length density on prey abundance and macrofauna predator abundance was due to enhanced belowground plant biomass (Barry et al., 2019; Milcu et al., 2008; Eisenhauer et al., 2010a,b; Scherber et al., 2010). Moreover, macrofauna predators seem to be more related to the response of mesofauna prey to changes in root length density than to that of mesofauna predators. This could be due to the fact that mesofauna predators in the sampled communities of this study were mainly comprised of Gamasina mites, which may preferably feed on nematodes, insect larvae, and Collembola with various degrees of specialization (Koehler, 1999).

The other resource acquisition trait, leaf area (LA), also had a positive effect on mesofauna prey abundance. It has been shown that traits associated with the leaf economic spectrum (e.g. specific leaf area or leaf dry matter content) can be related to soil functioning (e.g. decomposition; Garnier et al., 2004; Lavorel and Garnier, 2002; or, nitrification; Laughlin, 2011). In the species pool of the TBE, grass species tended to have a smaller leaf area than forb species (Ebeling et al., 2014); grass species in the Jena Experiment have a higher leaf dry matter content than forbs (Bachmann et al., 2018), which could explain the relationship of leaf size with the traits of the leaf economics spectrum. Based on these previous findings, it stands to reason that leaf traits should have indirect effects on soil communities through changes in soil properties and processes, such that increases in soil carbon or nitrification positively influence resources of detritivorous mesofauna.

4.5 Soil fauna responses to temporal resource acquisition traits

An important plant trait for soil fauna identified by our analysis was growth start (GS, Hypothesis 3). We found that a later start of plant growth (i.e. an increase in CWM growth start) had a negative effect on macrofauna abundance and species richness. While it is important to note that our assessment of soil fauna was limited to a single sampling event in early fall (September), variation in temporal plant traits such as growth start may still reliably indicate differences in the productivity of the plant community across the growing season. There are multiple examples from temperate grasslands to tropical forests showing that soil community composition, population dynamics, and plant community effects on soil biota vary over time (e.g. Eisenhauer et al., 2009; Moche et al., 2015). Bearing that in mind, a single snapshot measurement may not be able to clearly determine if temporal plant traits modify soil communities or just shift community dynamics in time. However, the significant effect of temporal plant traits found in this study suggests that multiple assessments of soil communities within and across seasons and years are required to more comprehensively study plant community effects on soil fauna (Berg and Bengtsson, 2007; Eisenhauer et al., 2018; Moche et al., 2015).

5. Conclusions

This study suggests that soil fauna abundance and diversity are better explained by plant trait identity and, to a lesser extent, trait diversity than by plant species richness. However, the effects of plant traits were not always consistent and depended on the soil fauna group in question. Our results further suggest that future studies should take into account multiple root traits (Laliberté, 2016) as well as their plasticity in responses to abiotic and biotic drivers (Eisenhauer and Powell, 2017) to better predict plant community effects on soil biota and functions. This study reveals, for the first time, the importance of temporal plant traits for soil fauna, highlighting the need for repeated assessments that cover the temporal dynamics of communities across different seasons (Dombos et al., 2017; Eisenhauer et al., 2018).

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