

Seasonal shifts in plant diversity effects on aboveground-belowground phenological synchrony

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INTRODUCTION

Compelling evidence shows that biodiversity enhances essential ecosystem functions, such as productivity and decomposition rates (Loreau & Hector 2001; Hooper et al., 2005; Cardinale et al., 2012). One primary underlying reason may be that individual species or groups of species in different functional groups may have dissimilar niches (*niche complementarity effects*) which allow diverse communities to maximize resource utilization and minimize competition (Cardinale et al., 2011; Zuppinger-Dingley et al., 2014). In theory, such niche differences include temporal variation in biological activity (Ebeling et al., 2014), and species in a community can adjust the timing of their biological activity in such a way that they cover the longest possible time and/or use the resources from the largest possible space in the habitat. If phenological niche differences are high enough, they can affect the shape of the phenology at the community level. For instance, if a plant community is composed of species that grow in early spring, the aboveground growing season will be extended, compared with a community lacking those species (Ebeling et al., 2014; Rudolf, 2019). Therefore, species and functional group diversity can affect the timing of community-level productivity (*i.e.* community phenology) via temporal niche differentiation and/or increasing the probability of species with those traits to occur in the community (*selection effect*) (Loreau & Hector 2001). However, variation in phenology is primarily monitored at the species rather than community level. Moreover, phenological variation is typically attributed to changes in climate drivers, such as temperature and water supply (Wright and van Schaik 1994; Staggemeier et al., 2018), and has rarely been quantified as a response to changes in biodiversity (but see Wolf et al., 2017 and Guimarães-Steinike et al., 2019).

Most ecosystem processes are soil-related or even soil-dependent (Bardgett & van der Putten, 2014; Soliveres et al., 2016; Schuldt et al., 2018). However, phenology tends to be monitored on easily observed aboveground response variables, and evidence describing soil phenology is mostly lacking (Bonato Asato et al., 2023). This knowledge gap leads to uncertainty about how well soil properties and belowground processes (*i.e.* root growth and activity of soil organisms) are predicted by aboveground phenological strategies (Eisenhauer, 2012; Blume-Werry et al., 2015; Eisenhauer et al., 2018). Because shoots and roots are interdependent, tight synchrony of their responses to environmental drivers is often expected (Iversen et al., 2015; but see Blume-Werry et al., 2016). However, the role of biotic and abiotic constraints on this synchrony seems to vary significantly among ecosystems and plant types, ultimately affecting which organs grow first, faster, or remain active and alive longer. Moreover, plant (roots and shoots) processes are often assumed to indicate ecosystem functions driven by the activity of organisms at adjacent trophic levels, such as soil fauna, but this may not necessarily be the case. Hot moments (within-year events inducing high activity) in soil organism activity depend, in part, on inputs from root exudates or pulses of detrital inputs from senescent roots (Kuznyakov & Blagodatskaya 2015). However, the limited evidence from the field does not always confirm

plant-activity-based assumptions. For example, phenological monitoring of detritivore feeding activity during the growing season in oaks has shown both a negative and no correlation between feeding activity and oak branch production (Eisenhauer et al., 2018). In an experimental grassland, feeding activity rates decreased during the summer, when plant growth is usually high (Siebert et al., 2019; Sünemann et al., 2021). Evidence suggests that investments in shoot and root production are commonly not synchronous (e.g. Steinaker & Wilson 2008; Steinaker et al. 2010; Sloan et al. 2016; Blume-Werry et al. 2016), as well as the dynamics of soil organisms (Bonato Asato et al., 2023; Eisenhauer et al., 2018). However, we lack experimental evidence demonstrating whether changes in biodiversity may influence the predictability and synchronization of the dynamics above and below the ground.

Presently, two predominant conceptual frameworks delineate the interplay between biodiversity and the synchronization of ecosystem functions. On the one hand, ecosystem stability theory suggests that increasing biodiversity increases temporal asynchrony among populations and functions, which would be one of the primary mechanisms for positive diversity-stability relationships (Cardinale et al., 2013; Loreau & de Mazancourt 2013). In other words, temporal asynchrony is needed for a healthy (stable) ecosystem functioning. On the other hand, ecosystem coupling, as defined by Ochoa-Hueso et al. (2021) as "the orderly connections between the biotic and abiotic components of ecosystems across spaces and/or time", suggests the opposite: for more efficiently process, cycle, and transfer of energy and matter, a higher temporal coupling of populations and functions is needed. Under this point of view, temporal synchrony is required for more efficient ecosystem functioning, and monitoring the dynamics of one function or population can be used as an indicator of activity in the other. In both cases, disruptions such as biodiversity change, may affect key aboveground or belowground processes, leading to acceleration or delay of community phenology and desynchronization of ecosystem functions. Despite the potential importance of aboveground-belowground phenological synchrony, the current lack of studies concurrently monitoring shoot, root, and soil fauna dynamics has impeded a thorough understanding of the mechanisms by which changes in biological diversity may influence the responses of these affiliated processes.

Here, we examine how experimentally manipulated plant diversity influences the phenological patterns of shoot, root, and soil fauna dynamics (responses). In the framework of a long-term grassland biodiversity experiment (the Jena Experiment; Roscher et al. 2014; Weisser et al. 2017), using well-established methods (LiDAR, phenological cameras, minirhizotrons, bait-lamina strips), we measure ecosystem response variables that are often used to evaluate aboveground-belowground ecosystem functioning and biological activity in annual plant communities (e.g. plant community height, greenness, root production, and detritivore feeding activity) every two to three weeks over four seasons (one full year). We used these data to calculate yearly values for each response variable, phenological patterns, and synchrony between response variables. With this approach, we ask the following questions:

- 1) How does plant diversity affect the yearly accumulated values of aboveground plant traits and belowground activity? We expect that increasing plant diversity throughout the year enhances all response variables (Weisser et al. 2017; Mommer et al., 2015; Eisenhauer et al., 2010).
- 2) Does plant diversity affect intra-annual aboveground and belowground phenological patterns? We predict that plant community shoot dynamics will be concentrated in spring and summer, as usual in temperate regions. Root production should last longer than that of shoots, as found in other studies (Steinaker & Wilson 2008; Blume-Werry et al. 2016), even though it is not clear if this longer activity is driven by an earlier start of the production, a later end, or both. For detritivore feeding activity, we expect a peak in early spring due to high moisture and increased temperature and another peak in autumn, driven by the increased availability of resources by above- and belowground plant-derived inputs and high moisture.
- 3) Do changes in plant diversity affect the synchrony of shoot, root, or soil organism dynamics? We expect plant species richness and functional group richness to enhance aboveground-belowground activity, which could lead to either more or less synchronized patterns. If plant diversity drives enhanced functioning at different time points (e.g. advances plant growth and delays root senescence), we could see a negative diversity effect on synchrony.

4) Does the time of year influence the strength/direction/predictability of relationships between aboveground-belowground response variables? Because plant shoots are only active for a restricted period, we expect plant diversity effects to be most pronounced during the growing season (Guimarães-Steinike et al., 2019), while abiotic constraints might mostly drive belowground dynamics out of the growing season.

MATERIALS AND METHODS

The Jena Experiment

This study was conducted in the Jena Experiment (Roscher et al., 2014; Weisser et al. 2017). The study site is located in the floodplain of the River Saale in the north of Jena (Thuringia, Germany, 50°55' N, 11°35' E, 130 m a.s.l.). The soil is classified as Eutric Fluvisol, developed from up to 2 m-thick fluvial sediments that are almost free of stones. Soil texture changes gradually from sandy loam to silty clay with decreasing distance from the river (Steinbeiss et al., 2008). During the sampling period of this study (March 2021 to Feb 2022), air and soil characteristics were monitored daily at a meteorological station on site (Fig. 1).

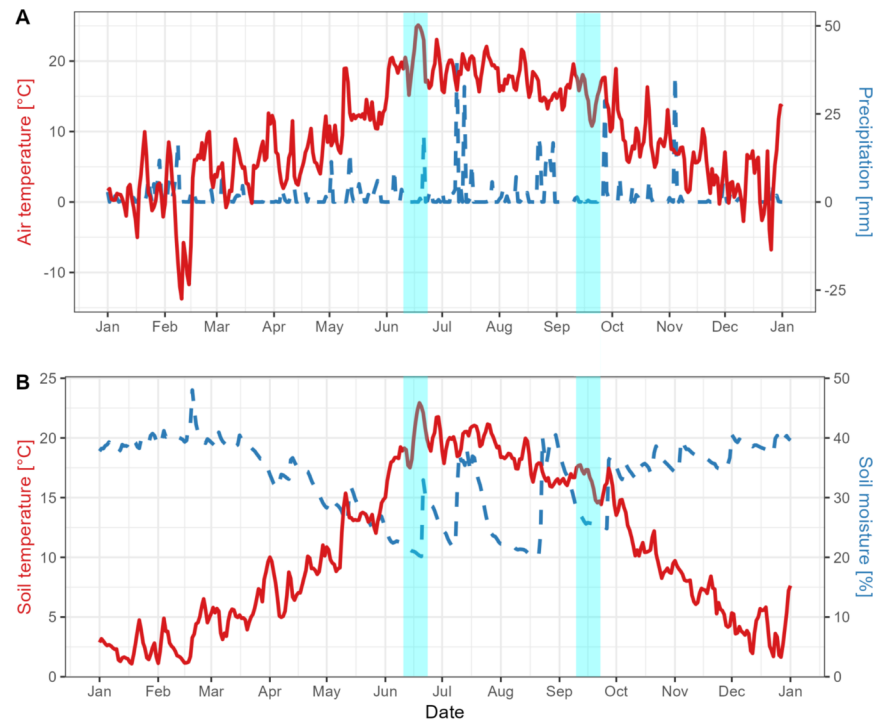


Fig. 1. Ombrothermic diagram of (A) air temperature at 2 m above the ground (continuous red line) and precipitation (dashed blue line) and (B) soil temperature (continuous red line) and soil moisture (dashed blue line) at 8 cm below the ground in 2021 and January 2022. The blue vertical stripes in June and September indicate the two mowing periods (14-25.06 and 13-24.09). Data source: local climatic station in the Jena Experiment.

Following a gradient in soil characteristics, the experiment was set up in four blocks containing an equal number of plots per plant diversity treatment within each block to avoid any confounding effects of soil heterogeneity. In total, the study site consists of 80 plots (~5.5 m × 6 m) that differ in levels of sown plant species richness (1, 2, 4, 8, 16, 60 species) and plant functional group richness (one to four of the functional

group: grasses, small herbs, tall herbs, legumes). Following common management practices in temperate extensively-used grasslands in Central Europe, where the Jena Experiment is located, the experiment was mowed twice. Moreover, the experimental plots were weeded three times during the study period to maintain the plot’s target species composition.

Temporal above- and belowground sampling

We sampled aboveground and belowground biological response variables biweekly (or every three weeks during winter). Even though the measurements’ definitions differ, e.g., plant community height would be better defined as a biological feature, and detritivore feeding activity is an activity rate, each measured response variable is commonly related to an ecological process (Table 1). We also present a simplified description of the sampling methods for each process. Please see the Supplemental Material for an extended version of the methods.

Table 1. Summary of sampling information and ecological meaning of each response variable.

Response variable	Ecological meaning
Plant Community Height	It is often correlated with leaf quality, longevity, and life-history traits. It is often used as a proxy for plant biomass.
Plant Greenness	It can be related to vegetation density, chlorophyll content, and photosynthetic activity and biomass.
Root Production	It is often related to soil carbon content, cycle, and capacity to acquire water and nutrients.
Detritivore Feeding Activity	Bait consumption is used as a proxy of detritivores’ feeding activity and is correlated with root biomass.

Statistical analyses

First, we tested the overall effects of plant species richness and plant functional group richness on the response variables using linear mixed models. Total values were calculated as the sum of each response during the entire sampling duration. We then tested the overall relationship between plant diversity and phenological synchrony. As a measure of phenological synchrony, we calculated Pearson’s correlation index (r) between all possible pairs of activities by plot (6 pairs in total). Correlations were calculated based on data collected during the maximum temporal extent possible; that is, for aboveground-aboveground and aboveground-belowground correlations for the entire growing season, and belowground-belowground correlations, for the entire year. Significant correlations are referred to here as positively or negatively coupled, when the direction of the correlation is positive and negative, respectively. A decoupled phenology here implies independence, i.e. non-significant relationships. We fitted individual linear mixed-effect models with the correlation coefficients as response and plant species richness or plant functional group richness as predictors. We treated block and plot as nested random factors for both analyses, and species richness was log-transformed.

To evaluate whether time of year altered plant diversity effects on the strength, direction, and predictability of relationships among aboveground and belowground response variables, we fit a series of mixed-effect models into a structural equation model (SEM; Grace, 2006; Eisenhauer et al., 2015), following the conceptual framework depicted in Fig. S1. Given that the response variables were sampled in different periods of the year, and differed in pattern (aboveground shoot responses were unimodal, while belowground responses were bi- or multimodal), we subset the dataset into three parts. The “spring” dataset encompasses the beginning of the aboveground measurements until the first mowing (14/Jul). The “summer” dataset encompasses the sampling after the first mowing until the second mowing, when the aboveground measurements finished (Fig. S1a). Finally, the “winter” dataset encompasses only belowground phenology, from the end of September until February (Fig. S1b). To simplify models and to avoid multicollinearity, we ran a stepwise selection of variables for each mixed-effect model within the SEM, using the ‘step’ function. The resulting models were then used to build the initial SEM, using the piecewiseSEM package (Lefcheck, 2015). We inspected the initial SEM model results according to the goodness-of-fit tests for both the SEM and individual causal relationships

and selected the final model by excluding the insignificant factors and adding missing relationships that significantly improved the model's global fit. We treated block and plot as nested random factors, allowing responses to vary randomly between blocks and plots. Given that samples taken from closer sampling point times are more alike, we also accounted for temporal autocorrelation fitting a 'corCAR1' term in each model. The variables mean plant community height, root production, and species richness were log-transformed. Due to the relationship between species richness and functional group richness, we have also incorporated correlated errors between those variables. We assessed the homogeneity of residuals with residuals vs. fitted values plots and Q-Q plots for data normality using 'Pearson' correlation (Zuur et al., 2009) for each of the mixed-effect equations used in the SEM. Statistical analyses were performed with R v. 4.2.2 (R Core Team, 2022).

RESULTS

Overall phenological patterns of aboveground and belowground processes

Shoots were active between March and September. Shoot height and greenness peaked in mid-spring but showed a slightly decoupled pattern (Fig. 2). Plant community height increased rapidly from May to June, until the first mowing. Plants re-started growing at a slower pace, and reached a lower maximum height before the second mowing in September (Fig. 2a). In contrast, plant greenness increased slowly in March, reached a stable peak across June, July, and August, and dropped suddenly in September (Fig. 2b). Interestingly, plant greenness was not affected by the mowing events (see Fig. S2 for a daily variation of greenness). Root production started in December, peaking in May, and senescing in summer (Fig. 2c). Already in March, root growth exceeded the values attained later during the summer months after the first mowing. Detritivore feeding activity showed two broad peaks - the first one in late spring and mid-summer, and a second one in early winter (Fig. 2d). The belowground data showed that soil fauna was much more variable, probably due to higher sensitivity to short-term climate fluctuation than shoots. In general, plant species richness and plant functional group richness increased total shoot (except greenness), root, and soil fauna activity (plant species richness only; Table S1).

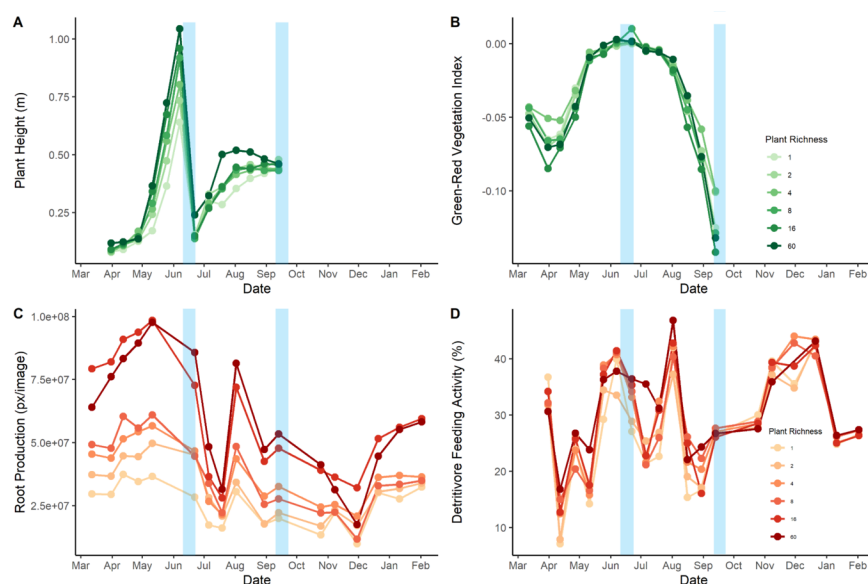


Fig. 2. Phenology of plant and soil processes in response to plant diversity treatments in the Jena Experiment. The phenology of (A) plant height, (B) greenness, (C) root production, and (D)

detritivore feeding activity from March 2021 to September 2021 for aboveground activity, and to February 2022 for belowground activity. The lines show the average monthly value for each species-richness level, with darker shades of green (aboveground) and brown (belowground) indicating higher plant species richness. The blue transparent stripes indicate the two mowing periods (14-25.06 and 13-24.09).

Plant diversity effects on the synchrony of aboveground-belowground phenology

Plant species richness affected the phenological synchrony of several response variables (Fig. 3), especially during the early growing season in spring (pre-mowing, Fig. 3a, b). Plant species richness increased phenological synchrony between plant community height and greenness, plant community height and root production, and greenness and root production. In contrast, plant functional group richness reduced phenological synchrony between greenness and root production and plant community height and detritivore feeding activity. This can be seen as a shift from negative r values to r values around zero. During summer (post-mowing period, Fig. 3b, e), increasing species richness shifted the synchrony between plant community height and greenness from a light asynchrony to a light-positive synchronous pattern. However, increasing plant functional group richness decoupled greenness and detritivore feeding activity (*i.e.* shift toward no correlation between response variables) (Fig. 3e). No significant plant diversity effects on phenological synchrony were observed over winter (Fig. 3c, f).

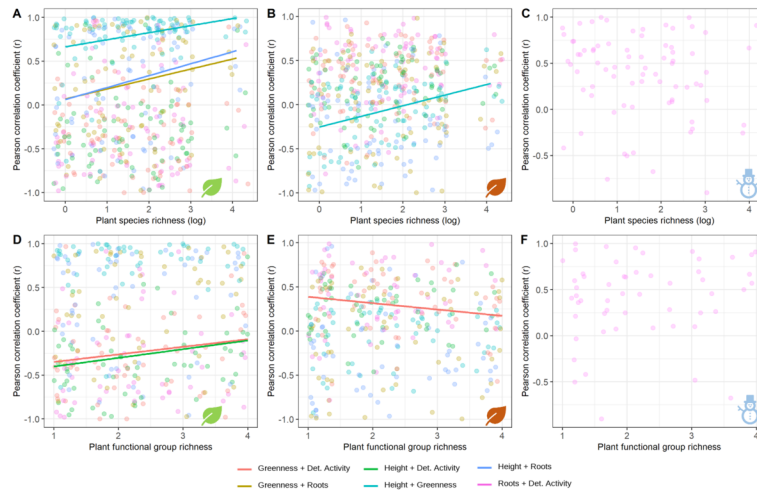


Fig. 3. Plant species richness (above) and plant functional group richness (below) effects on the phenological synchrony above and belowground dynamics. The first column (A, D) refers to the spring (pre-mowing) period, the middle column (B, E) refers to the summer (post-mowing) period, and the third column (C, F) refers to the winter period. Only significant ($p < 0.05$) relationships are shown (solid lines). Each point refers to one plot. For the full results, please see Table S2.

Seasonal effects of plant diversity and abiotic factors on aboveground and belowground responses

We tested the direct and indirect effects (*via* soil microclimate) of plant diversity (*i.e.* species richness and functional group richness) on plants and soils. Across the seasonal cycle, the timing of events above and below the ground was markedly influenced by the interplay of plant diversity and abiotic dynamics. However, across the seasons, these influences shifted in strength and direction.

During spring (Fig. 5a), richer communities showed higher plants, with increased root growth and enhanced activity of detritivores, but with less plant greenness. Instead, plant greenness increased with soil temper-

ature, increasing root production and detritivore feeding activity. Plant functional group richness and soil moisture did not explain significant variation in response variables during spring. Plant community height was associated with all other activities - positively with greenness and root production, and negatively with detritivore feeding activity. Moving into summer (Fig. 5b), higher plant species richness corresponded to enhanced root production and detritivore activity. However, increased plant functional group richness was observed to decrease detritivore activity. Notably, the impacts of abiotic factors on all studied ecosystem processes were predominantly negative. Root growth declined with rising soil temperature and moisture, while detritivore activity decreased with increasing soil moisture. Communities with taller plants showed cooler soil temperatures and higher soil moisture content. Interestingly, in contrast to spring observations, taller plant communities favored detritivore activity during summer while reducing plant greenness. Moreover, greenness was found to affect detritivore activity positively. As winter approached (Fig. 5c), richer plant communities showed enhanced root growth and soil moisture retention. Conversely, increased root growth and detritivore activity were observed in colder soils. Surprisingly, root production decreased detritivore activity during this season.

All models fitted the data well (Fisher's C and p -values in Fig. 5). Plant height was only explained by a fixed term in the spring model (marginal $R^2 = 0.42$), but its variation was also explained by the random terms (conditional $R^2 = 0.45$). Greenness was explained only by the fixed terms (marginal and conditional $R^2 = 0.39$ in the spring and $R^2 = 0.05$ in the summer model). The variation of root production was greatly explained by fixed terms in all models (marginal $R^2 = 0.24, 0.32$, and 0.20 for spring, summer, and winter, respectively). Still, the random terms increased explanatory power greatly (conditional $R^2 = 0.90, 0.75$, and 0.64 for spring, summer, and winter, respectively). The variation in detritivore feeding activity explained by random terms decreased along the year (marginal $R^2 = 0.06$ and 0.30 for spring and summer; conditional $R^2 = 0.23$ and 0.37 for spring and summer, respectively), to the point that random terms increased explanatory power only slightly in winter (marginal and conditional $R^2 = 0.14$ and 0.15 , respectively).

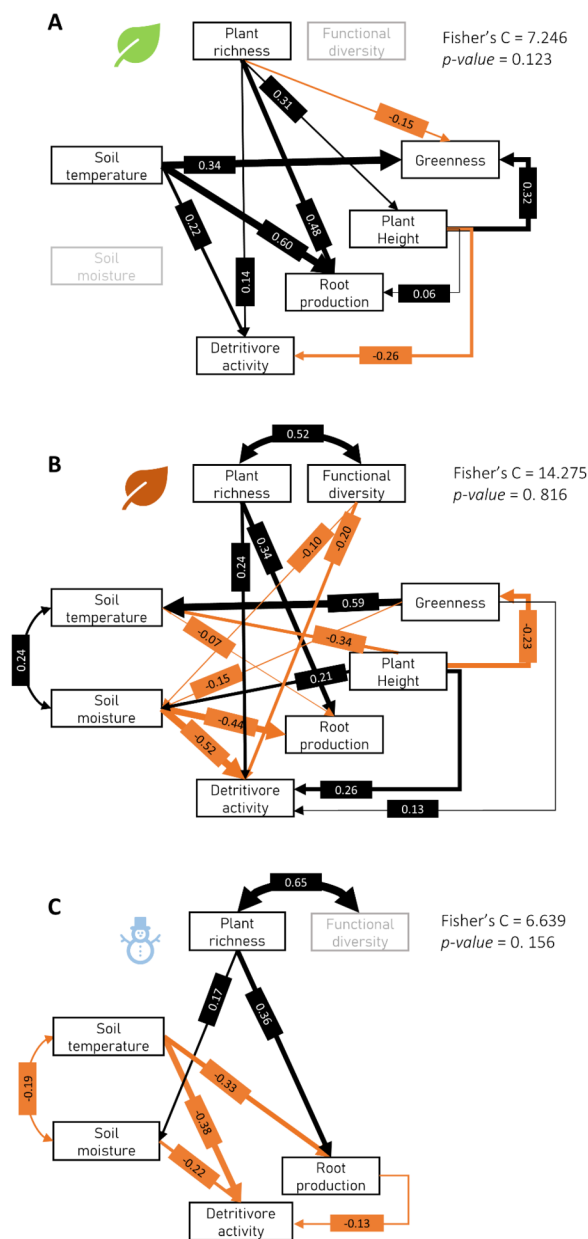


Fig. 5. The relationships between plant diversity, environmental factors, and plant and soil phenology in (A) spring, (B) summer, and (C) winter. Only significant ($p < 0.05$) paths are shown. The black arrows indicate positive effects, while the orange arrows indicate negative effects. The arrow width is proportional to the strength of the effect, which is indicated by the standardized coefficient in the boxes on the lines. Double-headed arrows indicate correlated errors.

DISCUSSION

Plant diversity effects of aboveground-belowground processes are present throughout the year

The magnitude and/or direction of the plant diversity effects on plant and soil processes changed throughout the year. This pinpoints phenology as a key, yet often overlooked, component of relationships between biodiversity and ecosystem functioning. On the one hand, plant diversity effects on overall plant height, root production, and detritivore feeding activity are consistent with previous works (Liang et al., 2016; Ma & Chen 2016; Birkhofer et al., 2011). On the other hand, the lack of plant diversity effects on overall greenness was unexpected, which may be explained by several reasons. One possible explanation is that the competitive environment in species-rich plant communities may be translated into enhanced flower production (Ebeling et al., 2008), decreasing greenness and suggesting the need to include more flower-related metrics to understand diversity effects on plant community production fully (Motohka et al., 2010; Schiefer et al., 2021). Another plausible explanation may be that greenness is in this case a better proxy of community structure aspects (Guimarães-Steinicke et al., 2019), such as density and volume, not representing photosynthetic activity well in our study (but see Muraoka et al., 2013). Furthermore, plant diversity effects on plant shoot production were shown in the first phase of the growing season, when diverse communities started growing earlier than previously observed (Guimarães-Steinicke et al., 2019). Given that other experiments are younger (as in the case of Guimarães-Steinicke et al., 2019), our results are consistent with the suggestion that temporal niche partitioning and legacy effects strengthen BEF relationships over time (Dietrich et al., 2021; Guerrero-Ramírez et al., 2017; Reich et al., 2012; Vogel et al., 2019).

Plant diversity effects on plant processes disappeared in summer when the positive effects of soil temperature were also absent. Instead, the plant community showed several effects on soil temperature and moisture during this period, including a buffer effect by plant height on soil temperature, as shown before (Huang et al., 2023). The direction of biotic-abiotic relationships is a classical discussion in Ecology (Mori et al., 2017). Several authors have debated whether biotic factors (e.g. plant structure) are driven by abiotic factors (e.g. soil temperature and moisture) or whether abiotic factors regulate diversity (Mori et al., 2017). Our results support both relationships and suggest that the strength and causal direction may change over the year even in the same community.

Belowground activity is high during winter

We found surprisingly high belowground activity in winter, revealing the influence of plant species richness and plant functional group richness on soil functioning. This is particularly important in grasslands, where roots account for about 70% of plant biomass (Jackson et al., 1996; Poorter et al., 2012). Root production in winter suggests that niche differences among species allow diverse communities to initiate growth at low temperatures, possibly resulting from a shift in carbon allocation to roots when temperature decreases (Poorter et al., 2012; Reich et al., 2014). Early onset of root production in a plant can convey a competitive advantage and diversify carbon allocation strategies (Harris 1977), which may, in turn, contribute to enhanced productivity of diverse plant communities during the aboveground growing season. The winter peak in detritivore feeding activity was unexpected, given that other works found low activities during winter (Sünnemann et al., 2021; Siebert et al., 2019, but see Gottschall et al., 2022). Plant diversity continuously enhanced detritivore feeding activity during spring and summer, but only functional group effects were observed in winter. Altogether, these results demonstrate that an accurate depiction of winter activity is required for a mechanistic description of temporal niche dispersion and biodiversity effects on ecosystem functioning (Gottschall et al., 2022).

Aboveground-belowground (a)synchrony along the seasons is mediated by plant diversity

Plant diversity effects on aboveground-belowground phenological synchrony shifted throughout the year, with independent impacts of plant species richness and functional groups shown. During spring, plant diversity generally increased phenological synchrony. Plant species richness enhanced height-greenness synchrony, indicating an optimal growth strategy, with the highest photosynthetic capacity reaching the timing of the highest physical structure (Zhao et al., 2022). During summer (post-mowing), height-greenness dynamics were asynchronous on average but showed a tendency towards positive synchrony with increasing species richness. This indicates that species-rich plant communities regrow faster after mowing, then plant height matches the high greenness. Plant diversity strongly enhanced height-root synchrony during spring, probably due to earlier shoot growth and extended root production in species-rich plant communities. Due to the high synchrony of height-greenness, roots were also synchronous with greenness in the same period. Even though plant functional richness was not a significant driver of above- and belowground activities in spring, it affected aboveground-belowground phenological synchrony. Specifically, greenness-feeding and height-feeding activity shifted from asynchrony in lower diversity to a non-correlation in higher diversity. This was the opposite in summer, when communities with higher plant functional group richness showed not synchronous greenness-feeding activity dynamics. This may reflect the negative effect of functional group richness on detritivore feeding activity alone in the same period, causing a mismatch with greenness that was still high. Even though detritivore feeding activity and root production were high in winter, their within-winter dynamics differed, resulting in non-correlated root growth-feeding activity dynamics.

CONCLUSIONS

The stimulating effects of plant diversity on plant biomass (Loreau & Hector 2001; Hooper et al., 2005; Cardinale et al., 2013; Liang et al., 2016), root productivity (Ma & Chen 2016; Ravenek et al., 2014; Oram et al., 2017), and soil fauna activity (Birkhofer et al., 2011; Spehn et al., 2000) have been shown before. However, our high temporal resolution data show that plant diversity effects on plant and soil processes change throughout the year. Root production is initiated during winter, right after the end of the aboveground growing season. With this, the positive plant diversity effects on aboveground processes may result from earlier plant diversity effects on the root system operating over winter. Unraveling the patterns of aboveground-belowground phenological synchrony offers a significant promise to advance underexplored areas of plant and soil ecology by adding an essential layer to understanding aboveground-belowground interactions (Ochoa-Hueso et al. 2021). In the context of biodiversity and ecosystem functioning, aboveground-belowground phenology may broadly advance the interpretation of species coexistence. It can help propose new mechanisms on whether and how biodiversity enhances ecosystem functioning. Overall, this work shows fundamental differences in the phenological patterns of leaf and root production and the activity of soil organisms, stressing the role of plant diversity in modulating the phenology of plant processes and soil fauna activity.

AUTHORS' CONTRIBUTION

AEBA, JH, NE, and CW conceptualized the paper. AEBA, CGS, and AE collected the data. CGS and TK processed the aboveground data, while GS and BS processed the belowground data with the input of SP, JD, TB, MS, and AEBA. AEBA statistically analyzed all the data, with the input of all authors. AEBA drafted the manuscript, with high inputs from JH. All authors revised and approved the final version of the manuscript.

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