

RESEARCH ARTICLE

Seasonal shifts in plant diversity effects on above-ground–below-ground phenological synchrony

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Abstract

1. The significance of biological diversity as a mechanism that optimizes niche breadth for resource acquisition and enhancing ecosystem functionality is well-established. However, a significant gap remains in exploring temporal niche breadth, particularly in the context of phenological aspects of community dynamics. This study takes a unique approach by examining plant phenology, which has traditionally been focused on above-ground assessments, and delving into the relatively unexplored realm of below-ground processes. As a result, the influence of biological diversity on the synchronization of above-ground and below-ground dynamics is brought to the forefront, providing a novel perspective on this complex relationship.
2. In this study, community traits (including plant height and greenness) and soil processes (such as root growth and detritivore feeding activity) were meticulously monitored at 2-week intervals over a year within an experimental grassland exhibiting a spectrum of plant diversity, ranging from monocultures to 60-species mixtures.
3. Our findings revealed that plant diversity increased yearly plant height, root growth and detritivore feeding activity, while enhancing the synchrony between above-ground traits and soil dynamics. Soil microclimate also played a role in shaping the phenology of these traits and processes. However, plant diversity and soil microclimate on above-ground traits and soil dynamics effects varied

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considerably in strength and direction across seasons, indicating a nuanced relationship between biodiversity, climate and ecosystem processes.

4. Notably, observations during the growing season unveiled a sequential pattern wherein peak plant community height preceded the onset of greenness. Meanwhile, root production commenced immediately after leaf senescence and persisted throughout winter. Although consistent throughout the year, detritivore activity exhibited pronounced peaks in the summer and late fall, albeit with notable variability.
5. *Synthesis*. The study underscores the dynamic interplay between plant diversity, above-ground–below-ground phenological patterns and ecosystem functioning. It suggests that plant diversity modulates above-ground–below-ground interdependence through intricate phenological dynamics, with the degree of synchrony fluctuating in response to the varying combination of processes and seasonal changes. Thus, by providing comprehensive within-year data, the research elucidates the fundamental disparities in phenological patterns across shoots, roots and soil fauna activities, thereby emphasizing the pivotal role of plant diversity in shaping ecosystem processes.

KEYWORDS

above-ground–below-ground interactions, biodiversity–ecosystem functioning, biological indicators, grasslands, soil ecology

1 | INTRODUCTION

Compelling evidence shows that biodiversity enhances essential ecosystem functions, such as productivity and decomposition rates (Cardinale et al., 2012; Hooper et al., 2005; Loreau & Hector, 2001). 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).

If phenological niche differences are high enough, they can affect the phenology at the community level. For instance, if a plant community is composed of species that grow in early and late-season, the above-ground growing season will be extended, compared with a community lacking those species (Ebeling et al., 2014; Rudolf, 2019). Therefore, over time, differences among taxa can affect the timing of community-level productivity via temporal niche differentiation (*complementarity effects*) and/or increasing the probability of species with those traits to occur in the community (*sampling effect*) (Loreau & Hector, 2001). Those differences can be realized either as species diversity or functional group diversity. However, variation in phenology is primarily monitored at the species rather than community level (Richardson et al., 2007; Yang et al., 2023). Moreover, phenological variation is typically attributed to changes in climate drivers, such as temperature and rainfall (Staggemeier et al., 2018; Wright

& Van Schaik, 1994), and has rarely been quantified as a response to changes in biodiversity (but see Guimarães-Steinicke et al., 2019; Wolf et al., 2017).

Most ecosystem processes are soil-related or even soil-dependent (Bardgett & van der Putten, 2014; Schuldt et al., 2018; Soliveres et al., 2016). However, phenology tends to be monitored on easily observed above-ground response variables (Albert et al., 2019; Huo et al., 2022), and evidence describing soil (below-ground plant parts and soil organisms) phenology is mostly lacking (Bonato Asato et al., 2023). 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. 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 (Kuzuyakov & Blagodatskaya, 2015). However, the limited evidence from the field does not always confirm plant-activity-based assumptions, such as expected high growth and activity in spring and summer (Eisenhauer et al., 2018; Siebert et al., 2018, 2019; Sünnemann et al., 2021). Instead, evidence suggests that investments in shoot and root production are

commonly not synchronous (e.g. Blume-Werry et al., 2016; Qu et al., 2024; Sloan et al., 2016; Steinaker et al., 2010; Steinaker & Wilson, 2008), 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 plant diversity 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 (a)synchrony 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 within a trophic level (Cardinale et al., 2013; Loreau & de Mazancourt, 2013). That is, temporal asynchrony is needed for a healthy (stable) ecosystem functioning. However, ecosystem processes operate across trophic levels. Therefore, 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' presents a multi-trophic alternative to evaluate efficient ecosystem processes, cycles and transfer of energy and matter. A higher temporal coupling of populations and functions indicates more efficient ecosystem functioning. Moreover, 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 above-ground or below-ground processes, leading to acceleration or delay of community phenology and asynchronization of ecosystem functions. Despite the potential importance of above-ground–below-ground 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 detritivore feeding activity. In the framework of a long-term grassland biodiversity experiment (the Jena Experiment; Roscher et al., 2004; Weisser et al., 2017), using well-established methods (LiDAR, phenological cameras, minirhizotrons, bait-lamina strips), we measured the indicators of above-ground–below-ground ecosystem functioning and biological activity in annual plant communities (i.e., plant community height, greenness, root production and detritivore feeding activity) every 2–3 weeks over four seasons (i.e., spring, summer, autumn and winter) over a year. We used these data to calculate a total yearly value 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 above-ground shoot, root, or detritivore feeding activity as indexed by accumulation of values throughout an entire year? We expect that increasing plant diversity throughout the year enhances plant height (Weisser et al., 2017), plant greenness, root production
2. Does plant diversity visually affect seasonal above-ground and below-ground phenological patterns? We predict that diversity effects on plant community height and greenness will be concentrated in spring and summer, as usual in temperate regions (Staggemeier et al., 2018; Wang et al., 2023). Diversity effects on root production should last longer than that of shoots, as found in other studies (Blume-Werry et al., 2016; Steinaker & Wilson, 2008), 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 diversity effects to peak in early spring due to high moisture and increased temperature and another peak in autumn, driven by the increased availability of above- and below-ground plant detritus and high moisture.
3. Do changes in plant diversity affect the synchrony of shoot, root, or detritivore feeding activity dynamics? We expect plant diversity to enhance shoot, root and detritivore feeding activity, which could lead to either more or less synchronized patterns. If plant diversity enhances functioning at different time points (e.g., advances plant growth and delays root senescence), we could see a negative effect of diversity on phenological synchrony (e.g., between plant height and root growth).
4. Does the season influence the strength and direction of direct and indirect relationships between plant diversity, microclimate and shoot, root, or detritivore feeding activity? Because plant shoots are only active for a restricted period, we expect plant diversity effects to be most pronounced during the growing season (Guimarães-Steinicke et al., 2019), while abiotic constraints might mostly drive below-ground dynamics out of the growing season (Box 1).

2 | MATERIALS AND METHODS

2.1 | The Jena Experiment

This study was conducted in the Jena Experiment (Roscher et al., 2004; Weisser et al., 2017), 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 from silty clay to sandy loam 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 (Figure 2).

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

BOX 1 Illustrated glossary of key concepts.

Phenology. Although classic phenology is studied at the individual or populational level, biological events at the community level, such as leaf or root growth and senescence, flowering, or soil fauna activity can be monitored, predicted and related to weather and climate at the community level (Richardson et al., 2007; Yang et al., 2023). Here, we only use phenology as a community concept. This way, *plant phenology* refers to plant traits and/or activities of the plant community, while *soil phenology* refers to the activity of below-ground plant parts and/or soil organisms.

Phenological synchrony. The temporal convergence of phenological events (*sensu* Wang et al., 2016). Here, we use synchrony as a non-numeric concept but as a general evaluation based on the co-variation between two curves throughout the year. If two curves (e.g., plant greenness and plant height) co-vary together over time, synchrony will be higher. If not (e.g., plant height and detritivore feeding activity), synchrony will be lower.

Phenological coupling. How biotic ecosystem components are orderly connected (adapted from Ochoa-Hueso et al., 2021). Contrary to synchrony, which is a general concept throughout the year, we use coupling as a numeric concept to understand how much two phenologies are distant from each other at one point in time. If, at one point in time, two phenologies are distant from each other (e.g., plant height and detritivore feeding activity), we have minor coupling. If not (e.g., when both points are high or low), we have major coupling (Figure 1).

plots (~5.5 m × 6 m) that differ in levels of sown plant species richness (1, 2, 4, 8, 16 and 60 species) and plant functional group richness (one to four of the functional groups grasses, small herbs, tall herbs and 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. For detailed information on the design of the experiment and how the plots were established, please see Roscher et al. (2004).

2.2 | Temporal above- and below-ground sampling

We sampled plant height, plant greenness, root production and detritivore feeding activity biweekly (or every 3 weeks during winter). Even though the measurements' definitions differ, for example, 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.

2.3 | Statistical analyses

First, to understand the effects of plant species richness and plant functional group richness on ecosystem functioning (question 1), we fitted eight linear mixed models, using one predictor and one response variable per model. For these analyses, the values of each sampling time were compiled as the sum of each of all values for each response variable during the entire year. We treated the block as random factor and species richness were log-transformed to encompass the design of the experiment (Roscher et al., 2004).

Then, we tested the relationship between plant diversity and phenological synchrony (question 3). As a measure of phenological synchrony, we calculated Pearson's correlation index (*r*) between all possible pairs of activities by plot (six pairs in total). Correlations were calculated based on data collected during the maximum temporal extent possible; that is, for above-ground–above-ground and above-ground–below-ground correlations for the entire growing season, and below-ground–below-ground 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. We fitted individual linear mixed-effect models with the correlation coefficients as response and plant species richness or plant functional group richness as predictors.

To evaluate whether time of year altered plant diversity effects on the strength, and direction of relationships among above-ground and below-ground response variables (question 4), we fit a series of mixed-effect models into a structural equation model (SEM; Grace, 2006; Lefcheck, 2015), following the conceptual framework depicted in Figure S1. Given that the response variables were sampled across the entire year, and differed in pattern (above-ground shoot responses were unimodal, while below-ground responses were bi- or multimodal), we subset the dataset into three parts. The 'spring' dataset encompasses the beginning of the above-ground measurements until the first mowing (14 July). The 'summer' dataset encompasses the sampling after the first mowing until the second mowing, when the above-ground measurements finished (Figure S1a). Finally, the 'winter' dataset encompasses only below-ground phenology, from the end of September until February (Figure 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, prior to the inclusion in the SEM. 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. We selected the final model by excluding the insignificant factors and adding missing relationships

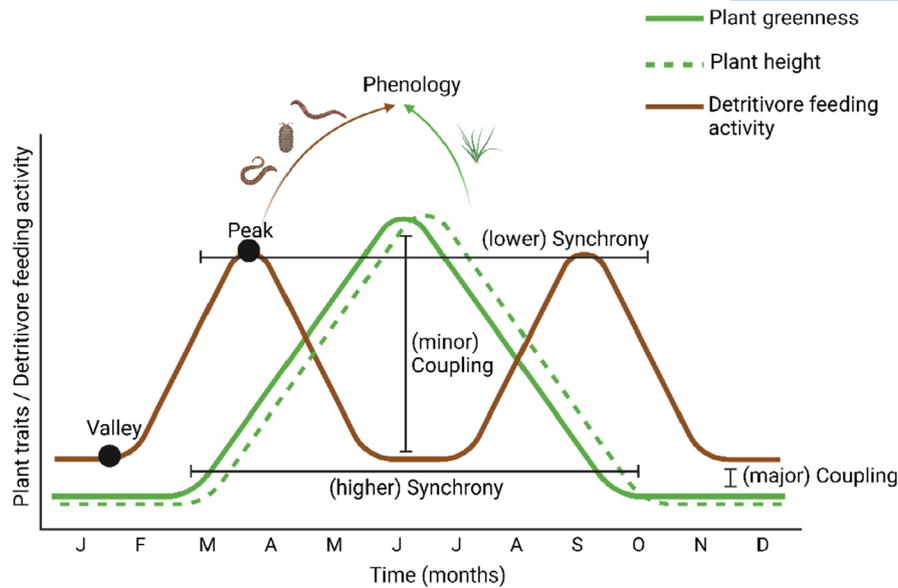
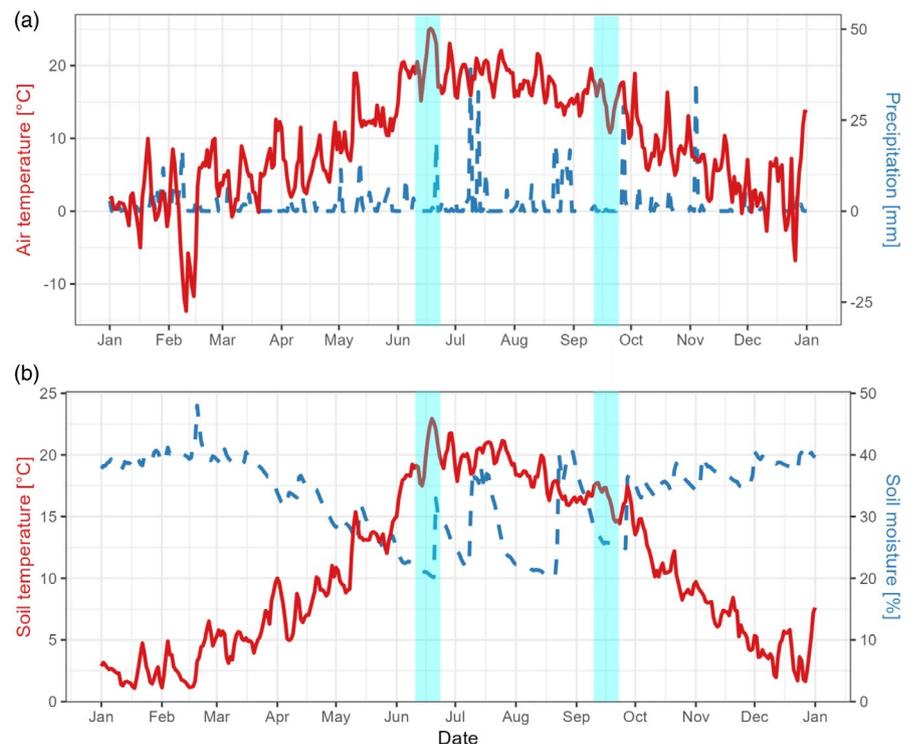


FIGURE 1 Conceptual representation of the key terms used in this work. Three representative phenologies are presented, two with similar patterns and another with a different pattern. In this example, plant greenness (depicted by the green solid line) and plant height (green dashed line) show higher synchrony if compared to any of those with detritivore feeding activity (brown solid line). The degree of coupling may vary depending on the sampling time (x-axis). In June, plant greenness is at its peak, while detritivore feeding activity is at its lowest, resulting in decreased phenological coupling. In November, however, both plant greenness and detritivore feeding activity are low, leading to high phenological coupling between them. Similarly, high phenological coupling would occur if both plant greenness and detritivore feeding activity were at their peaks.

FIGURE 2 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 June and 13–24 September). Data source: Local climatic station in the Jena Experiment.



that significantly improved the model's global fit. We treated block as random factor, allowing responses to vary randomly between blocks. 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, specifying it as plot nested

into block, to account for the repeated measurements at plot level. 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

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

Response variable	Ecological meaning	Sampling period	Simplified description
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 (Guimarães-Steinicke et al., 2019)	31 March to 13 September 2021	Using a terrestrial laser scanner (TLS), we generated 3D point clouds of the plot centre. The 3D point clouds were classified into soil and vegetation points, to further extract average plant community height (Guimarães-Steinicke et al., 2019)
Plant greenness	It can be related to vegetation density, chlorophyll content and photosynthetic activity and is normally used to detect leaf greening up and autumn colouring timing. (Cleland et al., 2006; Motohka et al., 2010)	31 March to 13 September 2021	We installed one phenological camera (Brinno TLC200) pointing to the centre of each plot corner. For each picture, we calculated the Green-Red Vegetation Index (GRVI) (Motohka et al., 2010; Yin et al., 2022)
Root production	It is often related to soil carbon content, cycle and capacity to acquire water and nutrients. It usually correlates to net primary productivity and soil fauna activity (McCormack et al., 2014; Ravenek et al., 2014)	10 March 2021 to 03 February 2022	We scanned each plot using minirhizotrons. We then identified the root pixels of each scan using a Neural Network and calculated the number of root pixels per scan (Ma & Chen, 2016; Ravenek et al., 2014)
Detritivore feeding activity	Bait consumption is used as a proxy of detritivores' feeding activity and is correlated with root exudation, decomposition rates and nutrient mineralization	26 February 2021 to 03 February 2022	In-situ decomposer feeding activity was measured using bait lamina strips, which are PVC sticks with 16 holes filled with cellulose-based bait. In each sampling period, old laminas were removed from the soil. The holes were rated as empty (all bait material was consumed, indicating high feeding activity), partly empty, or filled. Then, new laminas were inserted in the soil (Birkhofer et al., 2011; Eisenhauer et al., 2014)

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).

3 | RESULTS

3.1 | Overall phenological patterns of above-ground and below-ground processes (questions 1 and 2)

In general, plant diversity increased total shoot (except greenness), root and detritivore feeding activity (plant species richness only; Table S1). Shoots were active between May and September. Plant height and greenness peaked in mid-spring but showed a slightly asynchronous pattern (Figure 3). Plant 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 (Figure 3a). In contrast, plant greenness increased slowly in March, reached a stable peak across June,

July and August, and dropped suddenly in September (Figure 3b). Interestingly, plant greenness was not affected by the mowing events (see Figure S2 for a daily variation of greenness). Root production started in December, peaking in May and August, with a short but abrupt decrease in July (Figure 3c). 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 (Figure 3d). The below-ground data showed that detritivore feeding activity was much more variable, probably due to higher sensitivity to short-term climate fluctuation than shoots.

3.2 | Plant diversity effects on the synchrony of above-ground–below-ground phenology (question 3)

Plant species richness affected the phenological synchrony of several response variables (Figure 4), especially during the early growing season in spring (pre-mowing, Figure 4a,b). Plant species richness increased phenological synchrony between plant community height and greenness ($p=0.006$), plant community height

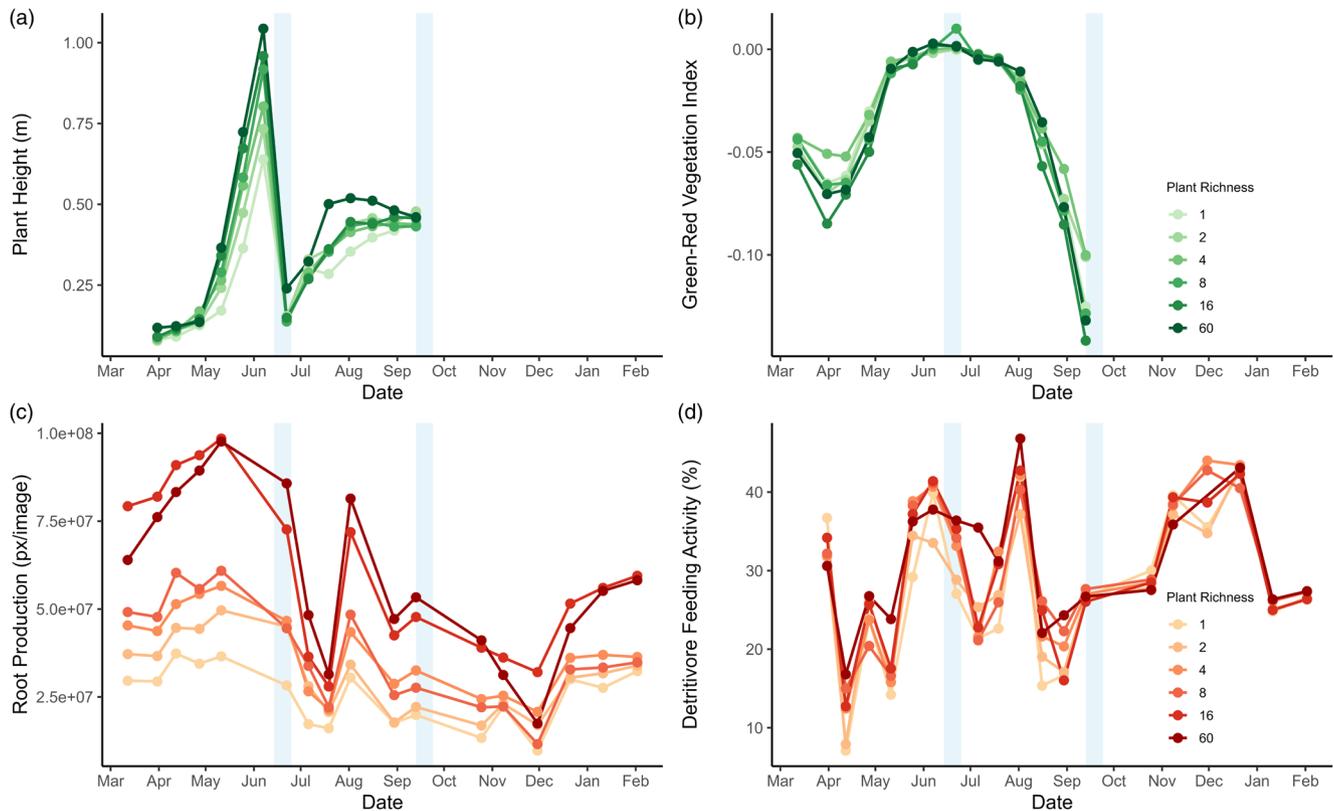


FIGURE 3 Phenology of plant and soil processes in response to plant diversity treatments in the Jena Experiment. The phenology of (a) plant height, (b) greenness, (c) root production and (d) detritivore feeding activity from March 2021 to September 2021 for above-ground activity, and to February 2022 for below-ground activity. The lines show the average monthly value for each species-richness level, with darker shades of green (above-ground) and brown (below-ground) indicating higher plant species richness. The blue transparent stripes indicate the two mowing periods (14–25 June and 13–24 September).

and root production ($p=0.026$) and greenness and root production ($p=0.042$). In contrast, plant functional group richness reduced phenological synchrony between greenness and detritivore feeding activity ($p=0.046$) and plant community height and detritivore feeding activity ($p=0.021$). This can be seen as a change from negative r values to r values around zero. During summer (post-mowing period, Figure 4b,e), increasing species richness shifted the synchrony between plant community height and greenness from non-significant to positive ($p<0.001$). However, increasing plant functional group richness shifted the correlation between greenness and detritivore feeding activity towards non-significance ($p=0.046$) (Figure 4e). No significant plant diversity effects on phenological synchrony were observed over winter (Figure 4c,f). Detailed results for each relationship can be seen in Table S2.

3.3 | Seasonal effects of plant diversity and abiotic factors on above-ground and below-ground responses (question 4)

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 (Figure 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 temperature, 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 (Figure 5b), higher plant species richness corresponded to enhanced root production and detritivore feeding activity. However, increased plant functional group richness was observed to directly decrease detritivore feeding activity, but to indirectly increase it via soil moisture (Figure 5b, $R^2=0.052$). 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 feeding 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 favoured detritivore feeding activity

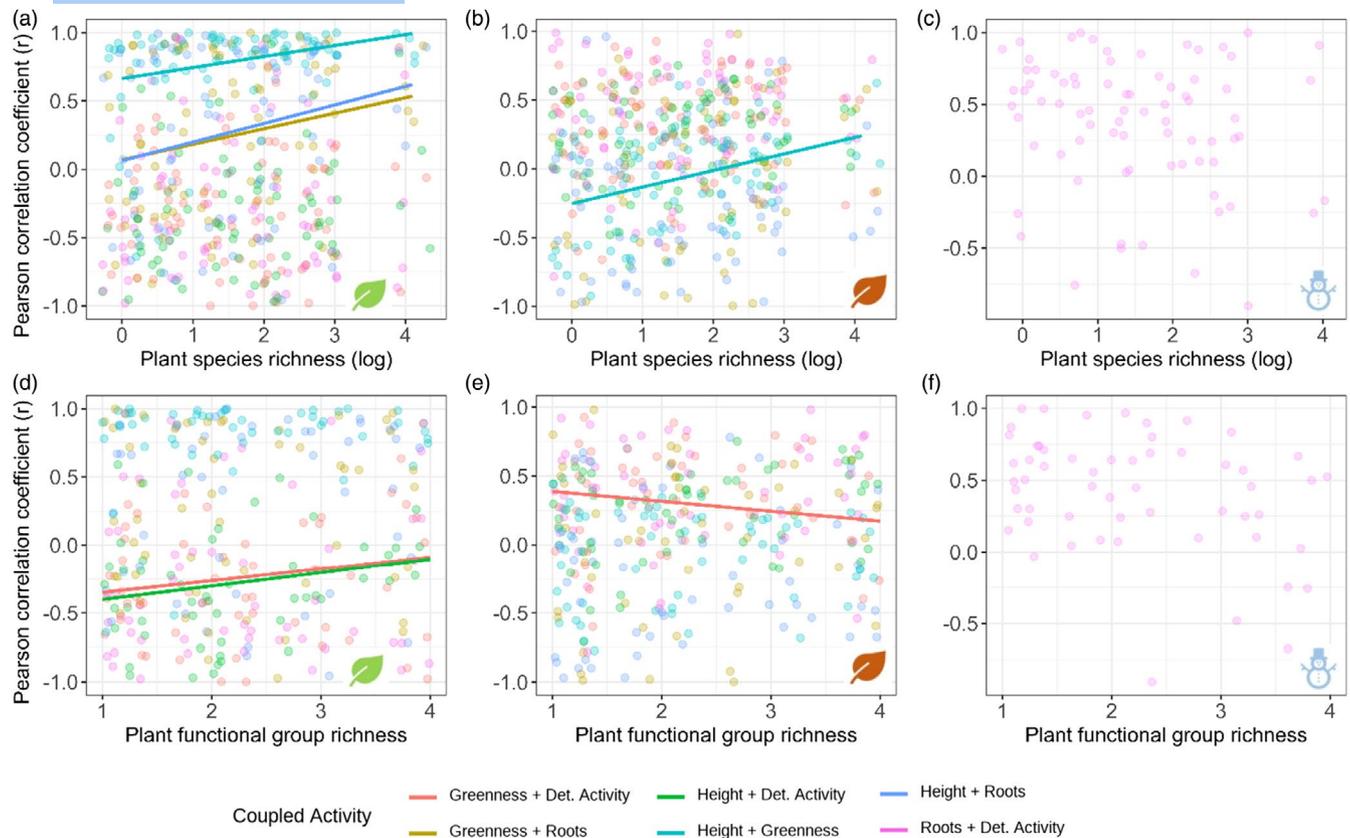


FIGURE 4 Plant species richness (above) and plant functional group richness (below) effects on the phenological synchrony above and below-ground dynamics. The first column (a, d) refers to the spring (pre-mowing) period, the middle column (b, e) refers to the summer (post-mowing) period, and the third 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](#).

during summer while reducing plant greenness. Moreover, greenness was found to affect detritivore feeding activity positively. As winter approached ([Figure 5c](#)), richer plant communities showed enhanced root growth and soil moisture retention. Conversely, increased root growth and detritivore feeding activity were observed in colder soils. Surprisingly, root production decreased detritivore feeding activity during this season. As in summer, plant diversity indirectly affected detritivore feeding activity via soil moisture, but this time from plant richness ([Figure 5c](#), $R^2 = -0.037$).

All models fitted the data well (Fisher's C and p -values in [Figure 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).

4 | DISCUSSION

4.1 | Plant diversity effects of above-ground–below-ground 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. Plant diversity effects on overall plant height, root production and detritivore feeding activity are consistent with previous works (Birkhofer et al., 2011; Liang et al., 2016; Ma & Chen, 2016). However, 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

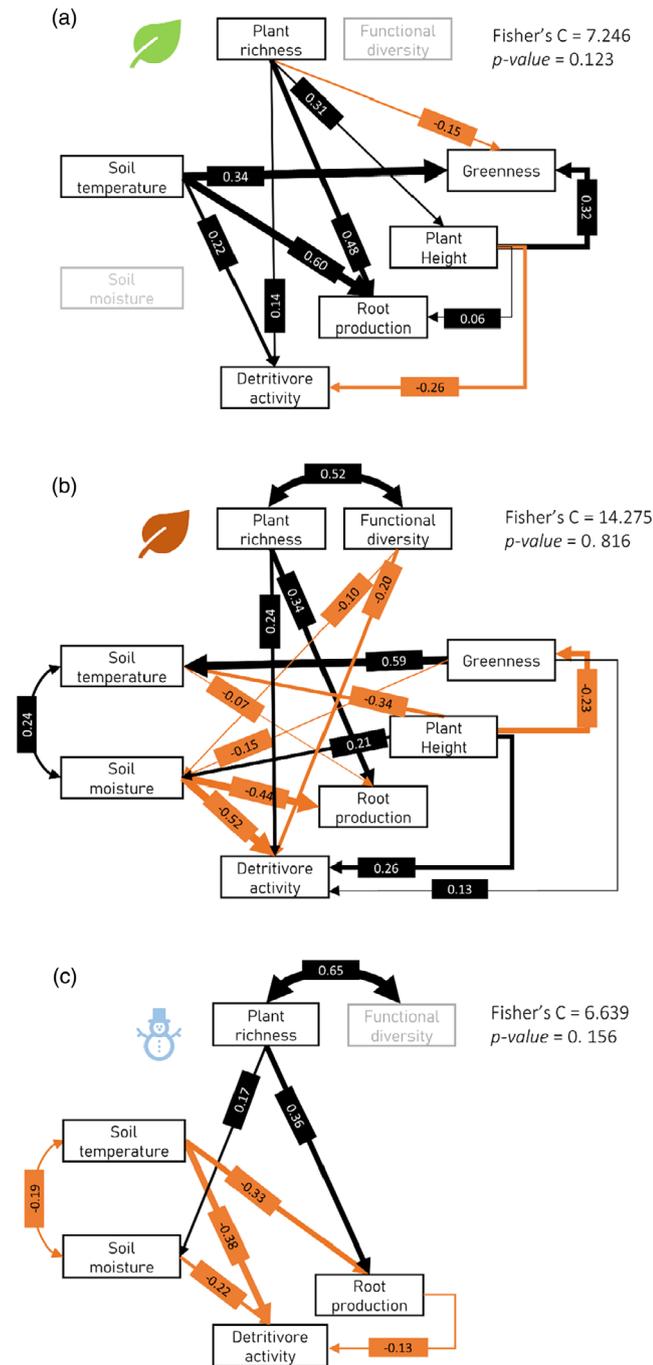


FIGURE 5 The relationships between plant diversity, environmental factors and plant and soil phenology in (a) spring, (b) summer and (c) winter. Only significant ($p < 0.05$) paths are shown. The black arrows indicate positive effects, while the orange arrows indicate negative effects. The arrow width 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.

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 the relationship between biodiversity and ecosystem functioning 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.

4.2 | Below-ground activity is high during winter

We found surprisingly high below-ground 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). Such high asynchrony with above-ground phenology was not expected but is partially in line with other studies that found decoupling between fine root production and shoot growth (Abramoff & Finzi, 2015; Huo et al., 2022; Qu et al., 2024; Tamura et al., 2022; Wang et al., 2023). 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 (Albert et al., 2019; Harris et al., 1977), which may, in turn, contribute to enhanced productivity of diverse plant communities during the above-ground growing season. The winter peak in detritivore feeding activity was unexpected, given that other works found low activities during winter (Siebert et al., 2018, 2019; Sünemann et al., 2021, 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).

4.3 | Above-ground–below-ground (a)synchrony along the seasons is mediated by plant diversity

Plant diversity effects on above-ground–below-ground phenological synchrony shifted across seasons, 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 (i.e. higher resilience, van Moorsel et al., 2021), 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 below-ground activities in spring, it affected above-ground–below-ground 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 no 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.

5 | CONCLUSIONS

The stimulating effects of plant diversity on plant biomass (Cardinale et al., 2013; Hooper et al., 2005; Liang et al., 2016; Loreau & Hector, 2001), root productivity (Ma & Chen, 2016; Oram et al., 2018; Ravenek et al., 2014) 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 above-ground growing season. With this, the positive plant diversity effects on above-ground processes may result from earlier plant diversity effects on the root system operating over winter. Unravelling the patterns of above-ground–below-ground phenological synchrony offers a significant promise to advance underexplored areas of plant and soil ecology by adding an essential layer to understanding above-ground–below-ground interactions

(Ochoa-Hueso et al., 2021). In the context of biodiversity and ecosystem functioning, above-ground–below-ground 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.

AUTHOR CONTRIBUTIONS

Ana Elizabeth Bonato Asato, Jes Hines, Nico Eisenhauer and Christian Wirth conceptualized the paper. Ana Elizabeth Bonato Asato, Claudia Guimarães-Steinicke and Anne Ebeling collected the data. Claudia Guimarães-Steinicke and Teja Kattenborn processed the above-ground data, while Gideon Stein and Berit Schreck processed the below-ground data with input from Stefan Posch, Joachim Denzler, Tim Büchner, Maha Shadaydeh and Ana Elizabeth Bonato Asato. Ana Elizabeth Bonato Asato statistically analysed all data, with input from all authors. Ana Elizabeth Bonato Asato drafted the manuscript, with high inputs from Jes Hines. All authors revised and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Jexis database at <https://doi.org/10.25829/C3BY-C712> (Bonato Asato et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Conceptual diagram of relationships informing structural equation models.

Figure S2: Daily variation of greenness (Green-Red Vegetation Index, GRVI) in the growing season 2021.

Figure S3: Spearman's correlations among response variables in spring (A), summer (B), and winter (C).

Table S1: Effects of plant species richness and plant functional group richness on the total activities.

Table S2: Effects of plant species richness and plant functional group richness on coupling in each season.

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