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RESEARCH ARTICLE

Home-field advantage, N-priming and precipitation independently govern litter decomposition in a plant diversity manipulation

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Abstract

1. Litter decomposition facilitates the recycling of often limiting resources, which may promote plant productivity responses to diversity, that is, overyielding. However, the direct relationship between decomposition, *k*, and overyielding remains underexplored in grassland diversity manipulations.
2. We test whether local adaptation of microbes, that is, home-field advantage (HFA), N-priming from plant inputs or precipitation drive decomposition and whether decomposition generates overyielding. Within a grassland diversity-manipulation, altering plant richness (1, 2, 3 and 6 species), composition (communities composed of plants from a single-family or multiple-families) and precipitation (50% and 150% ambient growing season precipitation), we conducted a litter decomposition experiment. In spring 2020, we deployed four replicate switchgrass, *Panicum virgatum*, litter bags (1.59 mm mesh opening), collecting them over 7 months to estimate litter *k*.
3. Precipitation was a strong, independent driver of decomposition. Switchgrass decomposition accelerated with grass richness and decelerated as phylogenetic dissimilarity from switchgrass increased, suggesting decomposition is fastest at 'home'. However, decomposition slowed with switchgrass density. In plots that contained switchgrass, we observed no relationship between decomposition and fungal saprotroph dissimilarity from switchgrass. However, in plots without switchgrass, decomposition slowed with increasing saprotroph dissimilarity from switchgrass. Combined these findings suggest that HFA is strongest when closely related neighbours, that is, heterospecific neighbours, are present in the community, rather than other individuals of the same species, that is, conspecifics. Legumes accelerated decomposition with more litter N remaining in those plots, suggesting that N-inputs from planted legumes are priming decomposition of litter C. However, decomposition and overyielding were unrelated in legume communities. While in grass communities, overyielding and decomposition were positively related and the relationship was strongest in plots with low densities of switchgrass, that is, with heterospecific neighbours.

4. Combined these findings suggest that plant species richness and community composition stimulate litter decomposition through multiple mechanisms, including N-priming, but only HFA from local adaptation of microbes on closely related species correlates with overyielding, likely through resource recycling. Our results link diversity with ecosystem processes facilitating above-ground productivity. Whether diversity loss will affect litter decomposition, productivity or both is contingent on resident plant traits and whether a locally adapted soil microbiome is maintained.

KEYWORDS
biodiversity–ecosystem function, grassland diversity manipulation, home-field advantage, litter decomposition, precipitation, priming, soil fungal saprotrophs, switchgrass

1 | INTRODUCTION

Decomposition of senesced organic material is an essential ecosystem process, facilitating the recycling of resources (Suseela & Tharayil, 2018; Wu et al., 2020; Zhang et al., 2023), including nitrogen (N) and phosphorus (P), which often limit productivity in terrestrial ecosystems (Du et al., 2020). Decomposition is one mechanism suggested to facilitate plant productivity increases with diversity, that is, overyielding (Zhang et al., 2023). While there is strong evidence precipitation (Epstein et al., 2002; Knops et al., 2001; Wu et al., 2020), litter identity (Hector et al., 2000) and diversity of litter types (Kou et al., 2020; Xiao et al., 2020; Zhang et al., 2023) alter decomposition, experiments exploring whether the diversity of planted species accelerates decomposition generate inconsistent results (Hättenschwiler et al., 2005; Knops et al., 2001; Milcu et al., 2008). These inconsistencies may occur because functional group and species richness are rarely independently manipulated, making it difficult to distinguish between diversity and functional group effects. Furthermore, the degree to which plant diversity and altered precipitation interact effecting litter decomposition remains underexplored in the context of biodiversity manipulation experiments; with decomposition rates, *k*, remaining unrepresented from grassland biodiversity manipulations (Xu et al., 2020).

Evidence precipitation alters leaf litter decomposition is robust (Austin & Vitousek, 2000; Knops et al., 2001; Wu et al., 2020). Water facilitates leaching of readily soluble compounds from litter (Swift et al., 1979). Additionally, water may also facilitate decomposition through interactions with biological communities. Soil moisture stimulates microbial community activity, which can in turn alter litter decomposition rates (Gui et al., 2017; Singh & Gupta, 1977). Precipitation and soil moisture changes may also alter soil microbial community composition (Allison et al., 2013; Zeglin et al., 2013), which could promote decomposition if saprotrophs able to break down that litter type become more abundant or active (Glassman et al., 2018; Gui et al., 2017). Native plant diversity can stimulate the development of diverse microbial communities, a pattern that is stronger with greater precipitation (Delavaux et al., 2021). However, interactive effects of precipitation and other drivers of decomposition, for example, plant diversity and community composition, remain underexplored.

While it is postulated litter diversity and enhanced N recycling from accelerated decomposition may help generate overyielding (Xiao et al., 2020; Zhang et al., 2023), litter decomposition dependence on plant diversity has been inconsistent in diversity manipulations (Hättenschwiler et al., 2005; Hector et al., 2000; Knops et al., 2001). With diversity, beneficial saprotrophs, specifically soil fungi and bacteria, may be diluted or inhibited by competitors, slowing decomposition (Gui et al., 2017; Hättenschwiler et al., 2005; Zhang et al., 2023). In this case, decomposition is expected to decrease with saprotroph diversity. By contrast, plant diversity may increase substrate diversity, promoting specialization (Hättenschwiler et al., 2005), thus generating a positive relationship between decomposition and saprotroph diversity. While plant richness has been difficult to link to faster decomposition in grassland diversity manipulations, plant community composition and functional type (e.g. graminoid, legume or non-leguminous forb) have consistent effects on litter decomposition (Hector et al., 2000; Knops et al., 2001). Two potential hypotheses explaining how functional group may facilitate litter decomposition are through local adaptation of saprotrophs on abundant plants (home-field advantage [HFA]; Gholz et al., 2000), and through their influence on the environment, namely increasing resource availability via high-quality litter inputs (N-priming; Kuzyakov et al., 2000).

In ecosystems where resident plant and microbial communities coevolved, microbial communities are more likely to develop specialized pathways to break down compounds found in their co-occurring litter, thereby accelerating decomposition. Local adaptation of microbes is well-documented (Di Lonardo et al., 2018; Fanin et al., 2021; Gholz et al., 2000), and described as HFA. An alternative approach to reciprocal transplant experiments is testing HFA through the phylogenetic structure of microbiome adaptation (Barbe et al., 2018; Xiao et al., 2020), in which we expect decomposition to slow with the average community phylogenetic distance from the 'home' litter type. Additionally, plant functional group can explain litter decomposition (Barbe et al., 2018; Le Bagousse-Pinguet et al., 2021). Plant litter decomposes faster in communities containing multiple representatives from the same functional group as the litter (Barbe et al., 2018; Knops et al., 2001; McLaren & Turkington, 2009). Whether closely related neighbours rather than those of the same species—heterospecific versus conspecific—confer a benefit for decomposition via local adaptation of closely related species' microbiomes is underexplored. In this case, generalization of microbial saprotrophs on a particular functional group's litter, rather than specialization on a species, might generate HFA.

Alternatively, plant community composition can influence litter decomposition through environmental changes, specifically litter inputs; higher leaf N concentration, for example, legumes, may stimulate decomposition (Knops et al., 2001; Vinton & Goergen, 2006). Increased N availability in soil stimulates microbial activities, increasing microbial demand for resources. To meet resource requirements, microbes break down more stable C forms, a phenomenon known as 'priming' (Kuzyakov et al., 2000). Nitrogen additions, through unnatural (e.g. fertilizer, N deposition) or natural means, may alter decomposition (Di Lonardo et al., 2018; Kohmann et al., 2019). Fertilizer application may decouple plant–microbial interactions, degrading microbiomes (Egerton-Warburton et al., 2007), and indeed, N deposition can slow decomposition (Di Lonardo et al., 2018). Natural N fixation via rhizobia, which can form symbiotic relationships with legumes (family Fabaceae), may stimulate decomposition while maintaining healthy soil microbiomes. This may increase the likelihood of detecting additive or synergistic effects of N-priming and HFA on decomposition, which remains unclear.

Increased decomposition could, for instance, increase N and P retention from above-ground yields, which could contribute to overyielding (Zhang et al., 2023). Indeed, the presence of legumes, and N availability, has long been cited as a source of overyielding in biodiversity manipulations (Marquard et al., 2009; Milcu et al., 2008; Temperton et al., 2007). However, whether recycling of resources via litter decomposition contributes to overyielding remains untested. We address this and ask how these processes are affected by global change, specifically exploring how switchgrass, *Panicum virgatum*, litter decomposition is affected by precipitation, plant species identity, diversity and their interactions in a grassland diversity manipulation. Our experimental design uniquely manipulates diversity at two levels, altering planted richness and whether planted species are from the same or different families. This enables us to test whether plant functional group matters independent of richness. It also allows us to ask whether richness matters generally, or whether diversity within a plant family, rather than between families, alters the outcome, a question not previously addressed. We hypothesize precipitation will accelerate *k* (H1.1), interacting with diversity (H1.2). Where HFA governs decomposition, *k* will be greatest in communities containing switchgrass (H2). We hypothesize where N-priming drives decomposition, communities containing legumes will accelerate rates (H3). Where species richness accelerates decomposition, we hypothesize *k* will correlate with overyielding (H4).

2 | METHODS

2.1 | Rainfall and plant diversity manipulation

We performed leaf litter decomposition assays within a grassland biodiversity-manipulation (Figures S1 and S2) three years after establishment at the University of Kansas Field Station (Jefferson, Co., KS, 39.05° N, 95.19° W). This experiment manipulated precipitation, altering growing season irrigation rates to 150% and 50% ambient rainfall (1 April–31 October). During the winter (1 November–31 March), both treatments received ambient precipitation (Figure S2; Table S1). By Year 3, a history of high and low rainfall had been effectively established (detailed in Appendix S1) receiving on average 1134.3 and 549.4 mm of irrigation, respectively (Figure S3; Table S1).

We manipulated planted richness by selecting 1, 2, 3 or 6 species (Table S2, detailed description in S1) from a pool of 18 species commonly represented in native tallgrass prairies (Table S3). Switchgrass, *Panicum virgatum*, was one of the planted grasses and was selected for its leaf stoichiometry, which is midrange compared with other planted species (Table S3; Figure S4). We altered plant community composition by selecting species for diverse communities from the same plant family (Asteraceae are asters-Ast, Fabaceae are legumes-Leg, and Poaceae are grasses-Grs) or multiple families (Table S2). This allows us to determine the role family identity plays in driving decomposition. The two species mixtures capture all possible family combinations (Ast-Ast, Ast-Grs, Ast-Leg, Leg-Leg, Leg-Grs and Grs-Grs) within the experiment (the experimental set-up and maintenance is detailed in Appendix S1).

2.2 | Community dissimilarity from switchgrass

To determine plant and microbial community dissimilarity from switchgrass, we calculated the average plant phylogenetic distance and soil microbial decomposer dissimilarity from switchgrass. We constructed a phylogeny for all 18 species in our experiment (detailed in Appendix S1; Figure S5; Table S4). We then calculate the mean phylogenetic distance from switchgrass multiplying the realized density of each plant by the phylogenetic distance between that plant and switchgrass (Cadotte et al., 2012), summed for all planted species in the plot (Equation S1). Four soil cores (20 cm depth) were collected in November 2020, extracted for microbial DNA and sequenced to determine soil fungal saprotrophs and bacteria (detailed in Appendix S1). We then calculate mean microbial community dissimilarity from switchgrass accounting for the realized density of each plant, multiplying it by that plant's microbial community dissimilarity from switchgrass's, characterized using robust Aitchison PCA distances (Martino et al., 2019) and summed for all planted species in the plot (Equation S2).

2.3 | Litter bag construction, deployment, sample processing, and C and N concentration

We collected recently senesced switchgrass leaf litter growing adjacent the field plots at the Land Institute's Perennial Agricultural Project Field Station plots in Lawrence, KS (Douglas Co., 39.00° N, 95.32° W) in October 2019 (description in S1). Switchgrass litter was air-dried for 21 days and cut into approximately 2.54-cm strips. We weighed 2.5 g of litter into 10.16 × 10.16 cm mesh bags, 1.59 mm opening chosen to include mesofauna (Handa et al., 2014; Kou et al., 2020). We deployed four replicates per plot on 29 March 2020 approximately 0.3 m in from the plot centre from each of the NW, NE, SW, SE corners, assigning each bag a position a–d, respectively (Figure S2). Litter bags were placed on top of the soil, or thatch layer if present, prior to the spring plant emergence. We harvested one replicate 28, 84, 147 and 209 days after deployment randomly selecting the order (c, a, b, d; Figure S2). Each bag was placed in a zip-loc bag, transported to the laboratory on ice, washed, air-dried (21 days) and weighed.

To determine the total litter carbon (C) and N concentration, we ground litter samples into a homogenous powder from times zero and four. Samples were sent to Kansas State Soil and Plant Testing Lab for total C and N analysis via dry combustion. We used mean time zero litter C, N and C:N to calculate the difference in litter quality after 209 days of decomposition (difference C, N, C:N = $t_{4\,i} - \overline{t_0}$). The initial litter C, N and C:N was on average 39.2% ± 0.3%, 0.9% ± 0.1%, and 46.3 ± 3.5, respectively (Table S5).

2.4 | Determining litter *k*

To estimate decomposition (*k*), we fit negative exponential decay models (Schlesinger & Bernhardt, 2013; Singh & Gupta, 1977) to our data using nonlinear least squares regressions in R v. 4.1.1 (R Core Team, 2022):

$$\text{Mass remaining (g)} = \text{A}\,\text{e}^{-kt}, \tag{1}$$

where A is the initial mass of each litter bag (g), *k* is the rate of exponential decay (day^{-1}) and *t* is time (days; Figure S6). Estimates of A were initiated at 2.5 (the starting mass of material put in each bag) and *k* at 0 (null hypothesis). Exponential decay functions were fit with five points including time zero, though for 12 plots lines were fit with four points because one replicate was lost or damaged beyond usability (Table S6). Estimates for *k* and A, along with 95% confidence intervals surrounding the estimates, were retained. Estimates significantly differed from zero where the confidence intervals do not overlap with zero.

2.5 | Plant productivity and overyielding

Productivity above-ground was assessed in July 2020, peak biomass for tallgrass prairies in Kansas, by observing plot level cover measurements and harvesting of biomass strips from the 0.1 m^2 of the 2.25 m^2 plot. Plants from the biomass strips were sorted to species, oven-dried at 70°C for 5 days and weighed. Since planted cover and biomass strips are correlated (Figure S7; Pearson's $r > 0.76$), we use species-specific correlations to scale biomass to the plot level, which allows us to characterize community-level dynamics (g m^{-2}) while simultaneously minimizing disturbance to plots we wish to maintain long term (details in Appendix S1). We then use plant productivity to calculate overyielding, specifically defining overyielding as complementarity (Loreau & Hector, 2001):

$$CE = S\,\overline{\Delta RY}\,\overline{M}, \tag{2}$$

where S is the number of species, $\overline{\Delta RY}$ is mean change in relative yield for all species, $\overline{M}$ the mean monoculture yield for all species in a mixture. Complementarity is high when the productivity of many species is greater than expectations based on their growth individually.

2.6 | Statistical analysis

To test whether precipitation and plant composition confer a benefit on decomposition we fit a linear mixed effect model predicting switchgrass decomposition (*k*) by precipitation, species richness, plant community composition, their interactions and the realized density of switchgrass, a proxy for HFA, as fixed effects. All linear mixed effect models were fit with *lme4* v. 1.1-31 and *lmerTest* v. 3.1-3 packages (Bates et al., 2015; Kuznetsova et al., 2017), visualized regressions using the *visreg* v. 2.7.0 package (Breheny & Burchett, 2017), and include subblock as a random effect to account for non-independence of replicate plots within individual shelters. We performed all statistical analyses in R v. 4.1.1 (R Core Team, 2022). To further explore HFA as a possible driver of plant community effects on litter decomposition, we fit a linear mixed effect model predicting decomposition by precipitation, species richness, their interaction, including phylogenetic distance as a covariate. Phylogenetic distance and plant community composition inherently covary, as such we are unable to test plant identity effects (e.g. grasses, legume, aster or multiple family effects) and phylogenetic dissimilarity in the same model.

To explore how the presence of grasses and N-fixers alter switchgrass decomposition in diverse communities, we first performed a three-way additive analysis of variance (ANOVA). For all mixtures, we test whether the presence or absence of asters, legumes or grasses altered switchgrass decomposition. To test how interactions between families affected decomposition, we performed a one-way ANOVA on two species mixtures, which contain all possible family combinations (Ast-Ast, Ast-Grs, Ast-Leg, Leg-Leg, Leg-Grs and Grs-Grs). To determine which family combinations differed from others, we performed a Tukey's post hoc honest significant difference test and to test for normality of errors a Shapiro–Wilks test.

To test local adaptation of soil microbes as a driver of decomposition via HFA, we modelled the relationship between soil microbial saprotrophs and litter decomposition. We test the relationship between *k* and microbial diversity, richness and Shannon's *H*, using linear mixed effect models including fungal saprotroph and bacteria diversity, richness and Shannon's *H*, as fixed effects. To test whether HFA is conferred by heterospecifics or conspecifics, we used piecewise regressions ('broken-stick' models) using base R 'lm' function to characterize the relationship between *k* and dissimilarity of microbial communities, specifically of fungal saprotroph and bacteria communities, from that of switchgrass. We set the breakpoint in the regression model where the proportion switchgrass was greater than zero. This approach tests whether microbial communities conditioned on switchgrass and whether microbial communities that are more like those found with switchgrass confer a benefit for litter decomposition.

To explore the potential influence of N-priming on decomposition, we characterize the relationship between ΔN, ΔC:N and ΔC after 209 days in situ. We fit linear mixed effect models predicting the change in tissue N, C or C:N between time four and zero by *k*, plant community composition, including their interaction as fixed effects.

To test whether switchgrass litter decomposition generates overyielding through HFA or N-priming, for single-family grasses, where we saw evidence of HFA, we fit a linear mixed effect model ($N=28$) in which *k predicts* complementarity, including the planted switchgrass density, and their interaction as fixed effects. To test whether N-priming generates overyielding, for single-family legume communities, where we saw evidence of N-priming, we fit a linear mixed effect model predicting complementarity with *k* as a fixed effect ($N=28$). Decomposition, *k*, is scaled to facilitate comparison with complementarity.

3 | RESULTS

3.1 | Exponential decay and precipitation

We were able to detect switchgrass decomposition over the 2020 growing season (Figure S6; mean $k=0.00235$, mean 2.5%=CI 0.0132, mean 97.5% CI=0.00346, Figure S8b). Higher precipitation significantly increased switchgrass decomposition ($F_{[1.0,217.9]}=41.36$, $p<0.001$, Figure 1a) and precipitation effects operated independent of other treatments (no interactions in Table S7).

3.2 | Planted species richness and identity

Plant community composition altered whether *k* increased with species richness. Switchgrass litter decomposed fastest in plant communities composed of grasses and slowest in plant communities composed of asters ($F_{[3.0,218.4]}=4.59$, $p=0.004$; Figure 1b). The relationship between decomposition and richness depended on plant community composition ($F_{[3.0,221.2]}=3.19$, $p=0.02$; Table S7) was positive in multiple family mixtures and grass communities, but not present or negative in aster and legume communities (Figure 1b).

Closely related species accelerate switchgrass decomposition, while the presence of switchgrass did not enhance litter *k*. With

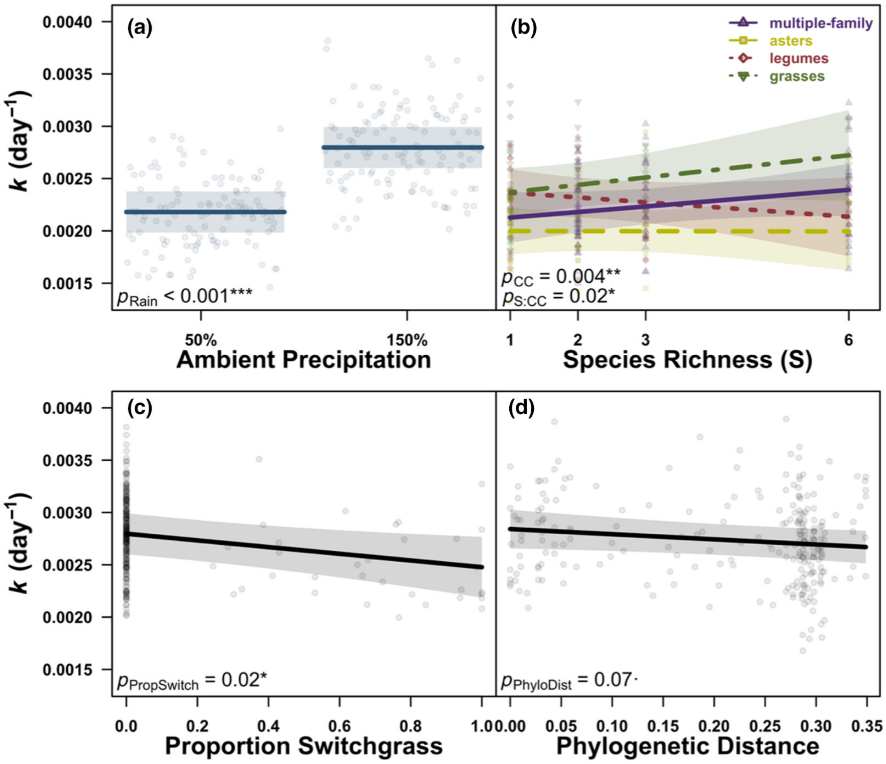

FIGURE 1 (a) Mean switchgrass decomposition rates under 50% and 150% ambient growing season rainfall. (b) The relationship between litter decomposition and plant species richness (S) by community composition (CC). (c) The relationship between decomposition and the realized proportion of switchgrass in mixture, and (d) decomposition and the plot average phylogenetic distance from switchgrass. $N=240$.

increased phylogenetic distance, *k* marginally increased (Figure 1c; $F_{[1.0,235.00]}=3.26$; $p=0.07$; Table S7). However, decomposition slowed as switchgrass densities increased ($F_{[1.0,221.43]}=5.89$; $p=0.02$; Figure 1b).

In mixtures (plant families ≥2), the presence of another grass or legume significantly accelerated decomposition (Figure 2B,C; Table S8), while the presence of an aster significantly slowed decomposition ($F_{[1,164]}=6.87$; $p=0.01$; Figure 2A; Table S8). In two species mixtures, switchgrass decomposed fastest in grass–grass combinations and significantly slower in aster–aster communities (Figure 2D; Table S9). In grass–aster mixtures, switchgrass decomposed at a similar rate as aster–aster combinations. Legumes accelerated decomposition independent of its neighbour. However, decomposition in legume–grass mixtures did not exceed decomposition observed in communities composed of two grasses or legumes.

3.3 | Microbial community dissimilarity from switchgrass

Decomposition decreased with microbial diversity and saprotroph community dissimilarity from switchgrass. Decomposition significantly decreased with fungal saprotroph diversity, Shannon's *H* (Figure 3b; Table S10) and marginally decreased with fungal saprotroph richness (Figure 3a; Table S10). No relationship was detected between decomposition and bacteria diversity (Figure S9a,b; Table S10). When switchgrass was not present in the community (switchgrass density = 0), decomposition decreased with fungal saprotroph community dissimilarity from switchgrass (Figure 3c; Table S11). When switchgrass was present in the community (switchgrass >0), no relationship was detectable between decomposition and fungal saprotroph community dissimilarity (Figure 3c; Table S11). A similar, but weak, pattern was observed for bacteria community dissimilarity and decomposition (Table S12; Figure S9c).

3.4 | Litter C and N concentration

After 209 days, switchgrass litter lost more C concentration relative to N. Litter ΔN tended to increase and was positively related to *k* (Figure 4a; Table S13); while litter consistently lost C after 209 days in situ, a pattern that marginally decreased with increased litter decomposition (Figure 4b; Table S13). These patterns resulted in a change in litter stoichiometry, generating a negative relationship between litter ΔC:N and *k* (Figure 4c; Table S13). This generally lowered litter C:N after 209 days in situ.

Plant community composition significantly altered litter ΔN and stoichiometry after 209 days of decomposition. Legume communities and those containing legumes (multiple family communities), had significantly more N remaining after 209 in situ (Figure 4d; Table S13), while litter in all functional groups had comparable ΔC (Figure 4e; Table S13). This resulted in a change in litter stoichiometry, such that litter decomposed with legumes had the lowest C:N (Figure 4f; Table S13), despite having high rates of decomposition (Figures 1b and 2b). We observed no significant interactions between community composition and *k* for ΔN, ΔC:N, or ΔC (Table S13).

3.5 | Productivity benefits associated with richness and litter *k*

Decomposition predicted overyielding, that is, complementarity, in communities containing all grasses with low densities of switchgrass.

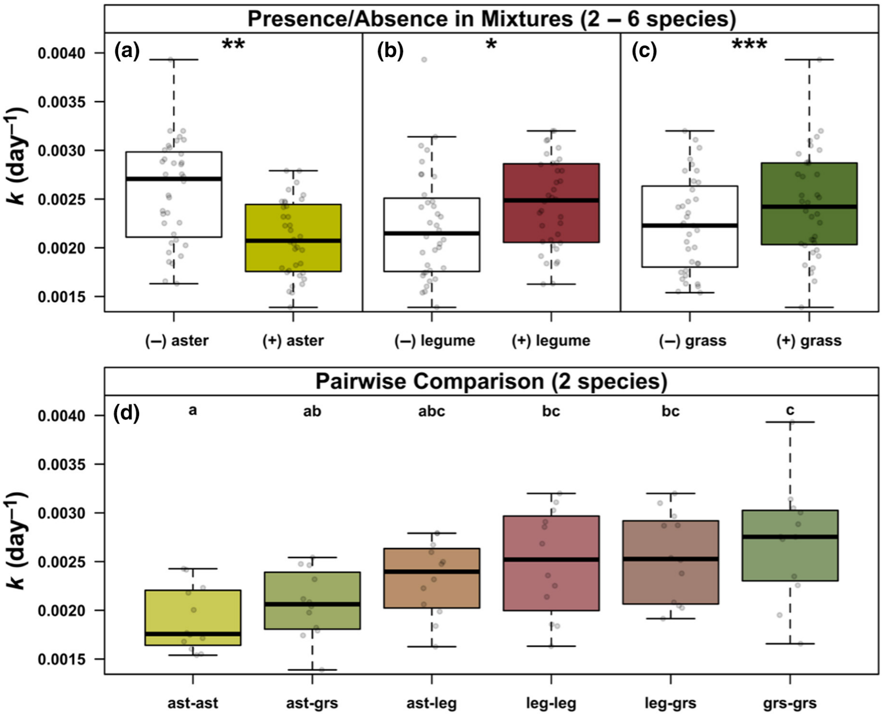

FIGURE 2 Boxplots of switchgrass decomposition (*k*) in mixtures with and without a species from the (A) aster, (B) legume, or (C) grass family. Stars indicate significant differences ($^{*}p \le 0.05$; $^{**}p \le 0.01$; $^{***}p \le 0.001$) between mixtures with and without the family determined by a three-way ANOVA, $N=168$. (D) Boxplots of switchgrass decomposition rates (*k*) by pairwise family combinations in mixtures containing two species. Different letters indicate significant differences between groups, as determined by a Tukey HSD post hoc test (ast—asters, leg—legumes and grs—grasses). $N=72$.

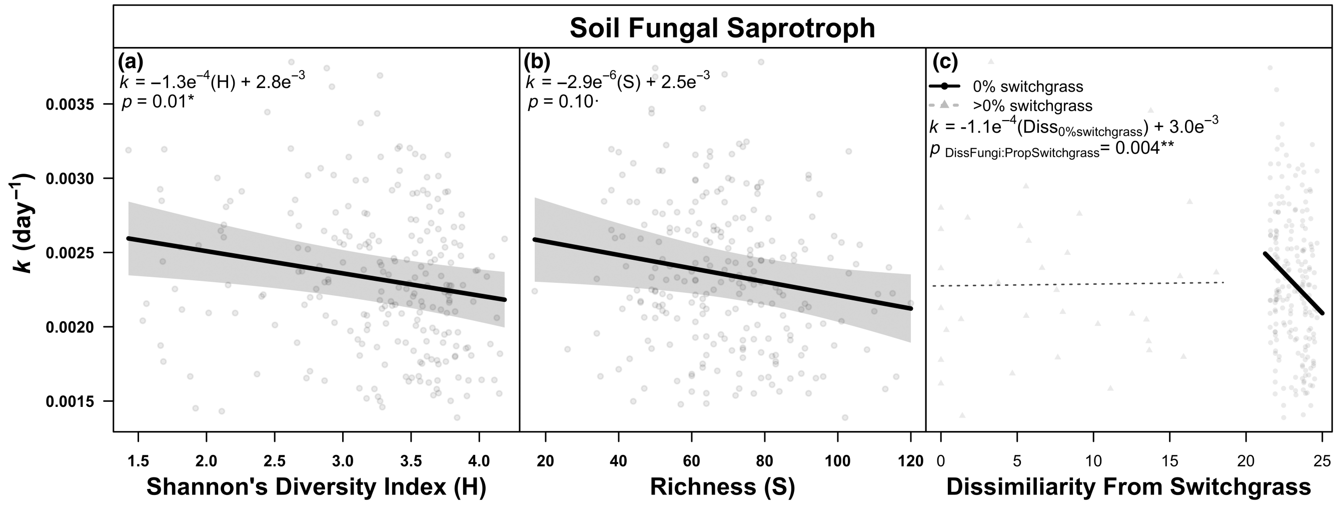

FIGURE 3 Linear relationship between litter decomposition and microbial diversity, (a) Shannon's *H* and (b) soil fungal saprotroph richness, with 95% confidence intervals around the regression represented by the grey bands. (c) The relationship between switchgrass decomposition and fungal saprotroph community dissimilarity from switchgrass.

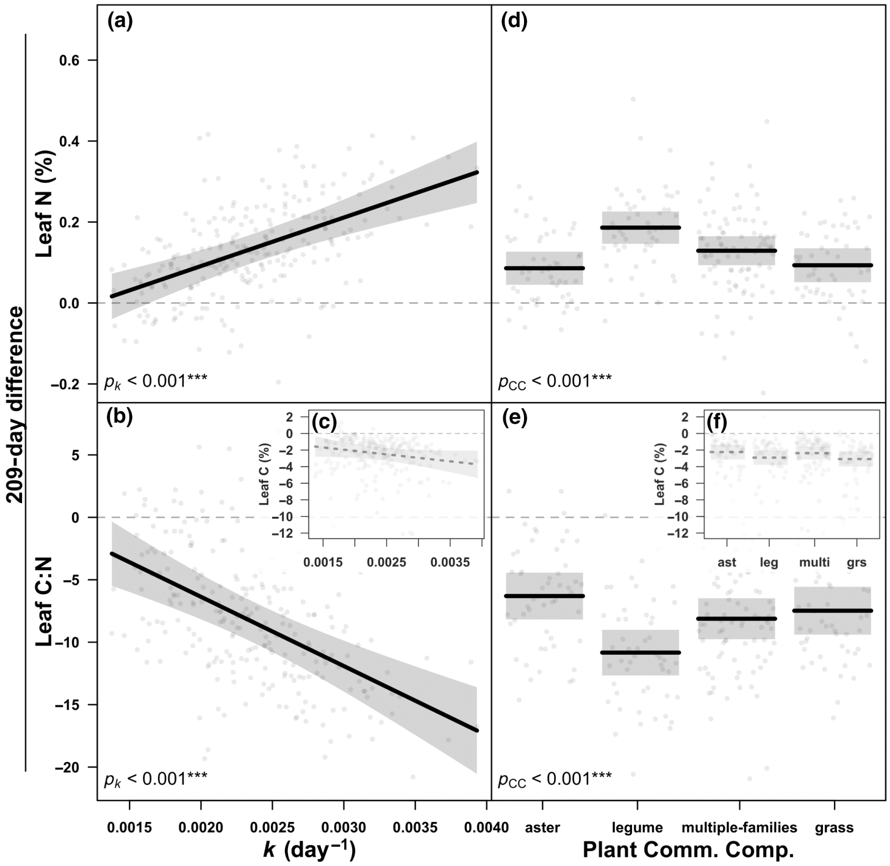

FIGURE 4 Relationship between switchgrass litter (a) ΔN, (b) ΔC:N, and (c) as the inset panel within panel (b), ΔC concentration and decomposition rates (*k*). Mean litter (d) ΔN, (e) ΔC:N, and (f) as the inset panel within panel (e), ΔC in communities composed of all asters, legumes, multiple-families, or all grasses. The 95% confidence intervals around the regressions and means are represented by the grey bands.

In single-family grass communities, we observed a significant positive relationship between *k* and complementarity (Table 1; Figure 5a) and a marginal interaction between switchgrass densities and *k*. The relationship between overyielding and *k* was strongest as switchgrass densities decreased in grass communities (Table 1; Figure 5b). In single-family legume communities, we observed no relationship between overyielding and decomposition (Table 1; Figure 5c), despite observing high decomposition (Figure 2b) and complementarity (Figure 5).

4 | DISCUSSION

Decomposition is a critical ecosystem process, maintaining ecosystem productivity and functioning. However, how plant diversity loss affects litter decomposition remains unclear (Xu et al., 2020). Litter decomposition is suggested to facilitate the strengthening relationship between richness and productivity that develops over time (Zhang et al., 2023). Here, we correlate decomposition

TABLE 1 Linear mixed effects model outputs of complementarity as a function of switchgrass decomposition rates (k), scaled for comparison to complementarity, as a fixed effect for all mixtures, community types containing 2–6 species, composed of only grasses (Grasses, $n=28$), and single-family legume mixtures (Legumes, $n=28$).

Complementarity ~	Grasses	Legumes
Fixed effects	($F_{[\text{NumDF,DenDF}]}$|Pr(>F)); p-value	
Scale(k)	$8.727_{[1.0,20.046]}$; **0.008****	$0.1199_{[1.0,22.592]}$; 0.73
Switchgrass	$5.804_{[1.0,21.861]}$; **0.02***	
Scale(k):switchgrass	$2.905_{[1.0,21.256]}$; 0.10·	
Random effects	(Variance (SD)|Pr(>|t|)); p-value	
Subblock	5.0 (2.2); **0.03***	18.0 (4.2); 0.20
Residual	8.4 (2.9)	21.0 (4.6)
Parameters	(Estimate (SD)|Pr(>chisq)); p-value	
(intercept)	0.67 (1.3); 0.63	5.1 (2.0); 0.08·
Scale(k)	2.5 (0.83); **0.008****	0.34 (0.98); 0.73
Switchgrass	10.0 (4.2); **0.02***	
Scale(k):switchgrass	−5.0 (3.0); 0.10·	

Note: To test heterospecific HFA, the expected density of switchgrass (switchgrass) is included in the Grass model. $\cdot p \leq 0.10$; $*p \leq 0.05$; $**p \leq 0.01$.

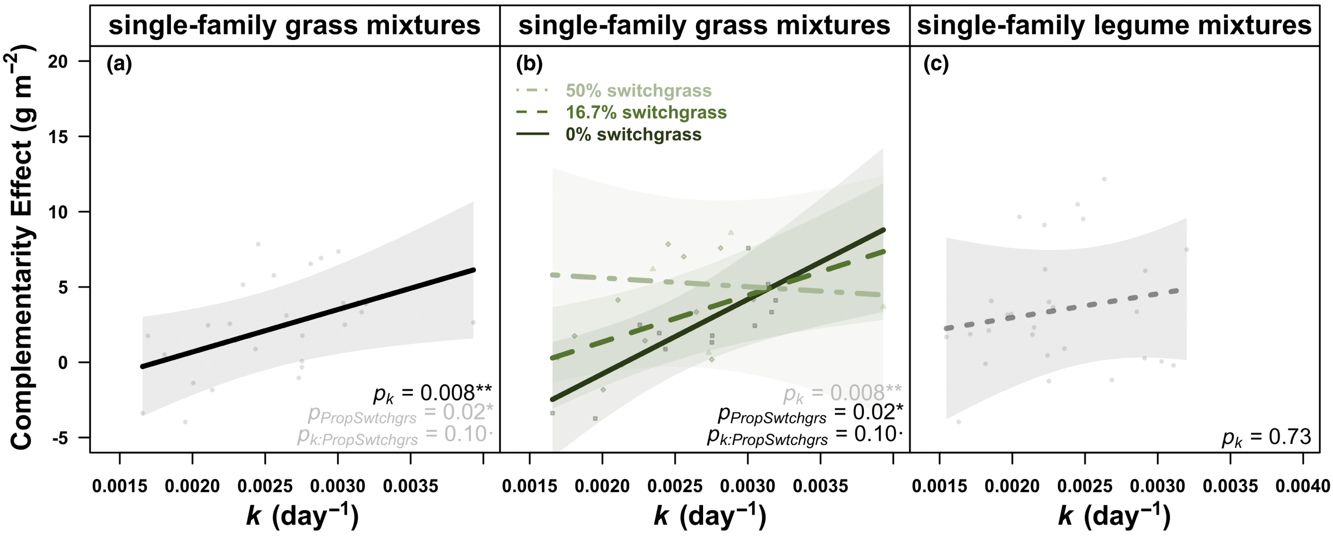

FIGURE 5 (a) The relationship between complementarity and litter decomposition in single-family grass mixtures, 2–6 species communities, $n=28$. (b) The relationship between complementarity and litter decomposition binned by the proportion of switchgrass in grass mixtures, $n=28$. Switchgrass bins are indicated for 0% switchgrass by the light green dot-dashed line, 16.7% switchgrass by the green dashed line, and 50% by the dark green solid line. (c) The relationship between complementarity and litter decomposition legume mixtures. $n=28$.

with productivity benefits associated with richness, confirming our hypothesis (H4), but observed within a growing season (Figure 5). Furthermore, we link these patterns with HFA through the local adaptation of microbial communities (Figure 3), one of the mechanisms driving litter decomposition. While N-priming from resident plants stimulates decomposition (Figure 2, confirming hypothesis H3) and alters the stoichiometry of decomposing litter (Figure 4), it does not correlate with overyielding. Precipitation also accelerates decomposition confirming hypothesis H1.1, but surprisingly occurred independent of plant richness and community composition (Figure 1) despite our expectations (H1.2). These findings suggest that HFA via local adaptation of microbes, N-priming from resident plants, and precipitation are stimulating the initial phases of litter decomposition, but surprisingly each is operating independently and only HFA correlates with concurrent above-ground productivity benefits from richness.

We link decomposition through HFA to positive overyielding observed within the same growing season, suggesting that the richness of closely related plants may positively affect above-ground productivity through rapid resource recycling. Previously indirect evidence, i.e. the addition of litter generating increased above-ground yields, suggests decomposition contributes to overyielding (Ma et al., 2022). We provide the first direct correlation between k and overyielding. Interestingly, we only find this positive relationship in diverse communities of grasses, and not in communities containing switchgrass in contrast with our expectations (H2). This resonates with previous work showing overyielding can arise rapidly, by the second year of the experiment, in the absence of legumes (van Ruijven & Berendse, 2005). Resource recycling was suggested to generate those patterns, as N use efficiency increased with richness, though whether through microbial decomposition of soil organic matter or recycling of plant litter remains unclear. Our work suggests increased rates of decomposition from locally adapted microbes are a possible explanation. Our findings also indicate richness of closely related species may generate overyielding, suggesting that richness in communities with relatively low trait diversity, or low phylogenetic diversity, can also generate overyielding and it is possible this operates through litter decomposition.

Surprisingly, increased decomposition via N-priming did not correlate with overyielding (Figure 5c). Resource partitioning has long been cited as the primary mechanism generating overyielding. While, there is evidence legumes (Marquard et al., 2009; Milcu et al., 2008; Temperton et al., 2007) and increased nitrogen use efficiency can correlate with overyielding (van Ruijven & Berendse, 2005), resource partitioning has been difficult to demonstrate in plant communities. A major challenge complicating quantifying resource partitioning is resource recycling within terrestrial ecosystems, which makes resource depletion particularly difficult measure. Here, we directly measure resource recycling and find the presence of high-quality litter increases *k*, but decomposition does not correlate with increased overyielding in legume communities (Figure 5c). Decomposition benefits for productivity could take time to accumulate. Even though N often limits plant productivity in temperate grasslands, in legume communities we found decomposing litter retained N relative to C, a pattern also observed in forests (Handa et al., 2014). This suggests that decomposition in legume communities may be generating increased productivity for soil microbial communities, as C is more often their limiting resource.

Switchgrass decomposition accelerated with species richness only in diverse grass communities, and generally increased with grasses. One might hypothesize sampling effects could generate this diversity effect, that is, switchgrass adapted saprotrophs combined with increased likelihood of including switchgrass in species rich grass communities. However, switchgrass decomposition slowed with increased switchgrass densities. Together, this confirms that switchgrass decomposition accelerates with increasing richness of closely related resident plants (i.e. other grasses), but not with switchgrass itself.

Furthermore, in communities containing switchgrass, we observed no relationship between fungal saprotroph dissimilarity from switchgrass and litter decomposition (Figure 3c). While no relationship was statistically detectable between bacteria community dissimilarity from switchgrass and decomposition, this was likely due to our inability to categorize bacteria into functional groups or guilds (Figure S9). Thus, it is notable that a similar pattern was observed, even if it was not statistically significant. These findings may appear in contrast with other studies, especially in tallgrass prairies, where decomposition is strongly enhanced by HFA where soil-microbial communities are conditioned to break down their own litter (Fanin et al., 2021; Gholz et al., 2000; Hossain & Sugiyama, 2020). However, the earliest descriptions of HFA describes the 'home-field' at a community level: HFA is broadleaf tree litter decomposing in broadleaf, as opposed to coniferous, forest soils (Gholz et al., 2000). Indeed, within our two-species comparisons (Figure 2d), depending on the group chosen, we sometimes detect HFA (grass–aster) and in other cases do not (grass–legume). Our findings suggest that HFA may more consistently be a community level, rather than species-specific, phenomenon.

Switchgrass litter decomposition was enhanced by legumes and litter lost more C relative to N from legume communities, providing strong evidence N-priming from resident plants stimulates litter decomposition. Generally, litter C:N decreased, suggesting that decomposition of switchgrass results in a loss of C relative to N. However, that was enhanced in communities composed of legumes, which had significantly lower litter C:N after 209 days decomposition, suggesting that legumes are stimulating decomposition of litter C. Legumes can form symbioses with N-fixing and tend to have higher tissue N concentration (Table S3), which can act as a natural fertilizer in N limited soils. While one study found N enrichment does not directly stimulate decomposition (Pichon et al., 2020), others suggest the addition of high-quality litter may stimulate the decomposition of low-quality litter by promoting microbes capable of mineralizing N, and altering decomposition of plant materials (Hossain & Sugiyama, 2020). The presence of N-fixing plants can likewise lower resource competition between soil microbial communities and plants, stimulating litter decomposition to facilitate microbial demands. Interestingly, we did not observe any additional benefit of having both a grass and legume in the community. Our results are consistent with previous studies (Zheng et al., 2023), though it is possible that our experimental design did not offer adequate power to detect additive or synergistic effects.

The presence of an aster in the community consistently slowed switchgrass decomposition (Figure 2a,d). Asters may promote microbial communities that inhibit the development of grass decomposing saprotrophs, as has been observed in other studies (Gui et al., 2017). This hypothesis is supported by the negative relationship we observed between fungal saprotroph dissimilarity and decomposition rates in communities without switchgrass (Figure 3c). Asters typically have high litter quality relative to grasses (Table S3) and may promote saprotrophic communities less able to break down litter with low quality. We observed a negative relationship between fungal saprotroph diversity and decomposition rates (Figure 3a,b), suggesting decomposition may have slowed from the dilution of microbial communities capable of decomposing grass litter.

Precipitation acts as an independent driver of decomposition in our study. These findings support many others describing the importance of water accelerating litter decomposition (Austin & Vitousek, 2000; Knops et al., 2001; Wu et al., 2020). We found no evidence that precipitation altered the dependence of litter decomposition on plant identity or richness. These findings suggest that physical mechanisms (i.e. leaching) could be generating increased decomposition with precipitation. Alternatively, favourably wet conditions could stimulate microbial activity, facilitating decomposition with precipitation. While we expect saprotrophic microbial community composition to change with both altered precipitation and plant community composition (Hättenschwiler et al., 2005; Zeglin et al., 2013), for this litter type over a single growing season, we did not observe significant interactions.

While it has been suggested that increased litter decomposition and resource recycling can generate overyielding, this hypothesis has remained poorly tested. We addressed this knowledge gap while additionally asking which mechanisms influence decomposition and teasing apart which mechanism facilitating decomposition also generates productivity–diversity relationships. We found local adaptation of microbiomes (HFA), N-priming and precipitation facilitate litter decomposition. However, we only find that plant diversity is correlated with litter decomposition, which in turn predicts overyielding in grass only plots, suggesting that HFA mediates productivity benefits with richness. Surprisingly, we found no evidence that resource recycling from legumes correlated with increased above-ground yields. Instead, our results suggest that N-priming is likely benefiting other guilds, that is, microbial communities. These findings not only link ecosystem processes to above-ground productivity, but also provide evidence regarding what type of diversity and through which mechanisms litter decomposition generates overyielding. Further work is necessary to determine how generalizable these patterns are among other plant groups and how these dynamics change over time. Decomposition benefits on productivity may be context dependent, as they were only evident in communities containing closely related species, that is, low functional trait or phylogenetic diversity, and are likely contingent on the presence of a healthy locally adapted soil microbiome.

AUTHOR CONTRIBUTIONS

LYP led manuscript writing, with all authors contributing to revisions. JDB designed the biodiversity manipulation experiment. LYP and JDB conceived of the litter decomposition experiment and performed statistical analyses. LYP conducted the field experiment, laboratory processing of samples and data processing and management. EBD constructed the plant phylogeny and generated phylogenetic distances. HMB generated microbial diversity and microbial community distances.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

We submitted DNA sequences to the NCBI Sequence Read Archive (SRA) under the accession number PRJNA1006419. The code associated with this manuscript is archived at https://doi.org/10.5281/zenodo.10523067. Data are provided at https://github.com/Lpodziko/RaD_LitterDecomposition_2020.git.

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REFERENCES

Allison, S. D., Lu, Y., Weihe, C., Goulden, M. L., Martiny, A. C., Treseder, K. K., & Martiny, J. B. (2013). Microbial abundance and composition influence litter decomposition response to environmental change. *Ecology*, *94*, 714–725.

Austin, A. T., & Vitousek, P. M. (2000). Precipitation, decomposition and litter decomposability of Metrosideros polymorpha in native forests on Hawai'i. *Journal of Ecology*, *88*, 129–138.

Barbe, L., Mony, C., Jung, V., Santonja, M., Bartish, I., & Prinzing, A. (2018). Functionally or phylogenetically distinct neighbours turn antagonism among decomposing litter species into synergy. *Journal of Ecology*, *106*, 1401–1414.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Breheny, P., & Burchett, W. (2017). Visualization of regression models using visreg. *The R Journal*, *9*, 56–71.

Cadotte, M. W., Dinnage, R., & Tilman, D. (2012). Phylogenetic diversity promotes ecosystem stability. *Ecology*, *93*, S223–S233.

Delavaux, C. S., Schemanski, J. L., House, G. L., Tipton, A. G., Sikes, B., & Bever, J. D. (2021). Root pathogen diversity and composition varies with climate in undisturbed grasslands, but less so in anthropogenically disturbed grasslands. *The ISME Journal*, *15*, 304–317.

Di Lonardo, D. P., Manrubia, M., De Boer, W., Zweers, H., Veen, G. F., & Van der Wal, A. (2018). Relationship between home-field advantage of litter decomposition and priming of soil organic matter. *Soil Biology and Biochemistry*, *126*, 49–56.

Du, E., Terrer, C., Pellegrini, A. F. A., Ahlström, A., van Lissa, C. J., Zhao, X., Xia, N., Wu, X., & Jackson, R. B. (2020). Global patterns of terrestrial nitrogen and phosphorus limitation. *Nature Geoscience*, *13*, 221–226.

Egerton-Warburton, L. M., Johnson, N. C., & Allen, E. B. (2007). Mycorrhizal community dynamics following nitrogen fertilization: A cross-site test in five grasslands. *Ecological Monographs*, *77*, 527–544.

Epstein, H. E., Burke, I. C., & Lauenroth, W. K. (2002). Regional patterns of decomposition and primary production rates in the U.S. Great Plains. *Ecology*, *83*, 320–327.

Fanin, N., Lin, D., Freschet, G. T., Keiser, A. D., Augusto, L., Wardle, D. A., & Veen, G. F. C. (2021). Home-field advantage of litter decomposition: From the phyllosphere to the soil. *The New Phytologist*, *231*, 1353–1358.

Gholz, H. L., Wedin, D. A., Smitherman, S. M., Harmon, M. E., & Parton, W. J. (2000). Long-term dynamics of pine and hardwood litter in contrasting environments: Toward a global model of decomposition. *Global Change Biology*, *6*, 751–765.

Glassman, S. I., Weihe, C., Li, J. H., Albright, M. B. N., Looby, C. I., Martiny, A. C., Treseder, K. K., Allison, S. D., & Martiny, J. B. H. (2018). Decomposition responses to climate depend on microbial community composition. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 11994–11999.

Gui, H., Hyde, K., Xu, J., & Mortimer, P. (2017). Arbuscular mycorrhiza enhance the rate of litter decomposition while inhibiting soil microbial community development. *Scientific Reports*, *7*, 42184.

Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., Chauvet, E., Gessner, M. O., Jabiol, J., Makkonen, M., McKie, B. G., Malmqvist, B., Peeters, E. T., Scheu, S., Schmid, B., van Ruijven, J., Vos, V. C., & Hattenschwiler, S. (2014). Consequences of biodiversity loss for litter decomposition across biomes. *Nature*, *509*, 218–221.

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *36*, 191–218.

Hector, A., Beale, A., Minns, A., Otway, S., & Lawton, J. (2000). Consequences of the reduction of plant diversity for litter decomposition: Effects through litter quality and microenvironment. *Oikos*, *90*, 357–371.

Hossain, M. Z., & Sugiyama, S. I. (2020). Relative importance of soil microbes and litter quality on decomposition and nitrogen cycling in grasslands. *Ecological Research*, *35*, 912–924.

Knops, J. M. H., Wedin, D., & Tilman, D. (2001). Biodiversity and decomposition in experimental grassland ecosystems. *Oecologia*, *126*, 429–433.

Kohmann, M. M., Sollenberger, L. E., Dubeux, J. C., Jr., Silveira, M. L., & Moreno, L. S. (2019). Legume proportion in grassland litter affects decomposition dynamics and nutrient mineralization. *Agronomy Journal*, *111*, 1079–1089.

Kou, L., Jiang, L., Hattenschwiler, S., Zhang, M. M., Niu, S. L., Fu, X. L., Dai, X. Q., Yan, H., Li, S. G., & Wang, H. M. (2020). Diversity-decomposition relationships in forests worldwide. *eLife*, *9*, e55813. https://doi.org/10.7554/eLife.55813

Kuznetsova, A., Brockhoff, P., & Christensen, R. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*, 1–26. https://doi.org/10.18637/jss.v082.i13

Kuzyakov, Y., Friedel, J., & Stahr, K. (2000). Review of mechanisms and quantification of priming effects. *Soil Biology and Biochemistry*, *32*, 1485–1498.

Le Bagousse-Pinguet, Y., Gross, N., Saiz, H., Maestre, F. T., Ruiz, S., Dacal, M., Asensio, S., Ochoa, V., Gozalo, B., Cornelissen, J. H. C., Deschamps, L., García, C., Maire, V., Milla, R., Salinas, N., Wang, J. T., Singh, B. K., & García-Palacios, P. (2021). Functional rarity and evenness are key facets of biodiversity to boost multifunctionality. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2019355118. https://doi.org/10.1073/pnas.2019355118

Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, *412*, 72–76.

Ma, Z. W., Zeng, Y. F., Wu, J., Zhou, Q. P., & Hou, F. J. (2022). Plant litter influences the temporal stability of plant community biomass in an alpine meadow by altering the stability and asynchrony of plant functional groups. *Functional Ecology*, *36*, 148–158.

Marquard, E., Weigelt, A., Temperton, V. M., Roscher, C., Schumacher, J., Buchmann, N., Fischer, M., Weisser, W. W., & Schmid, B. (2009). Plant species richness and functional composition drive overyielding in a six-year grassland experiment. *Ecology*, *90*, 3290–3302.

Martino, C., Morton, J. T., Marotz, C. A., Thompson, L. R., Tripathi, A., Knight, R., & Zengler, K. (2019). A novel sparse compositional technique reveals microbial perturbations. *MSystems*, *4*, e00016-19. https://doi.org/10.1128/mSystems.00016-19

McLaren, J. R., & Turkington, R. O. Y. (2009). Plant functional group identity differentially affects leaf and root decomposition. *Global Change Biology*, *16*, 3075–3084.

Milcu, A., Partsch, S., Scherber, C., Weisser, W. W., & Scheu, S. (2008). Earthworms and legumes control litter decomposition in a plant diversity gradient. *Ecology*, *89*, 1872–1882.

Pichon, N. A., Cappelli, S. L., Soliveres, S., Hölzel, N., Klaus, V. H., Kleinebecker, T., & Allan, E. (2020). Decomposition disentangled: A test of the multiple mechanisms by which nitrogen enrichment alters litter decomposition. *Functional Ecology*, *34*, 1485–1496.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Schlesinger, W. H., & Bernhardt, E. S. (2013). *Biogeochemistry: An analysis of global change*. Academic Press.

Singh, J., & Gupta, S. (1977). Plant decomposition and soil respiration in terrestrial ecosystems. *The Botanical Review*, *43*, 449–528.

Suseela, V., & Tharayil, N. (2018). Decoupling the direct and indirect effects of climate on plant litter decomposition: Accounting for stress-induced modifications in plant chemistry. *Global Change Biology*, *24*, 1428–1451.

Swift, M. J., Heal, O. W., Anderson, J. M., & Anderson, J. M. (1979). *Decomposition in terrestrial ecosystems*. University of California Press.

Temperton, V. M., Mwangi, P. N., Scherer-Lorenzen, M., Schmid, B., & Buchmann, N. (2007). Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. *Oecologia*, *151*, 190–205.

van Ruijven, J., & Berendse, F. (2005). Diversity-productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 695–700.

Vinton, M. A., & Goergen, E. M. (2006). Plant–soil feedbacks contribute to the persistence of *Bromus inermis* in tallgrass prairie. *Ecosystems*, *9*, 967–976.

Wu, Q., Yue, K., Wang, X., Ma, Y., & Li, Y. (2020). Differential responses of litter decomposition to warming, elevated CO_2, and changed precipitation regime. *Plant and Soil*, *455*, 155–169.

Xiao, W., Chen, C., Chen, X., Huang, Z., & Chen, H. Y. (2020). Functional and phylogenetic diversity promote litter decomposition across terrestrial ecosystems. *Global Ecology and Biogeography*, *29*, 2261–2272.

Xu, S., Eisenhauer, N., Ferlian, O., Zhang, J., Zhou, G., Lu, X., Liu, C., & Zhang, D. (2020). Species richness promotes ecosystem carbon storage: Evidence from biodiversity-ecosystem functioning experiments. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20202063.

Zeglin, L., Bottomley, P., Jumpponen, A., Rice, C., Arango, M., Lindsley, A., McGowan, A., Mfombep, P., & Myrold, D. (2013). Altered precipitation regime affects the function and composition of soil microbial communities on multiple time scales. *Ecology*, *94*, 2334–2345.

Zhang, W. P., Fornara, D., Yang, H., Yu, R. P., Callaway, R. M., & Li, L. (2023). Plant litter strengthens positive biodiversity-ecosystem functioning relationships over time. *Trends in Ecology & Evolution*, *38*, 473–484.

Zheng, J., Li, S., Wang, H., Dai, X., Meng, S., Jiang, L., Ma, N., Yan, H., Fu, X., & Kou, L. (2023). Home-field advantage meets priming effect in root decomposition: Implications for belowground carbon dynamics. *Functional Ecology*, *37*(3), 676–689. https://doi.org/10.1111/1365-2435.14251

SUPPORTING INFORMATION

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

Appendix S1: Methods.

Appendix S2: Figures and Tables.

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