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ORIGINAL ARTICLE

Plant functional diversity shapes soil respiration response to soil moisture availability

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ABSTRACT

Narrowing uncertainties associated with land–atmosphere carbon (C) fluxes is critical for projecting climate futures, but large uncertainties in modeling soil respiration (R_S) hinder progress. Difficulties accounting for how biological communities will respond to altered precipitation contribute to those uncertainties, but remain underexplored in situ. In a rainfall and grassland diversity manipulation experiment altering both plant richness and community composition, we measured R_S monthly for four growing seasons, along with multiple physical (soil moisture and temperature) and biological drivers (aboveground, root, and microbial biomass) of R_S. Relationships between plant richness and R_S were dependent on plant community composition and soil moisture conditions. Elevated R_S was associated with grass diversity, likely governed by enhanced soil moisture at 12 cm. Microbial biomass was the strongest independent predictor of R_S. Though soil moisture was a strong predictor of R_S, covariance with precipitation treatments and microbial biomass suggests it operated through multiple indirect pathways. Even after accounting for several R_S drivers, plant community composition and richness still accounted for a nontrivial amount of variation in R_S. This suggests that unexplored pathways associated with biological complexity (for example, microbial community composition) influence R_S. Finally, altered precipitation changed diversity-R_S relationships over time, suggesting that soil microbes can respond relatively rapidly to altered precipitation, perhaps due to the diversity of specialist microbes in our initial common soils. Our work demonstrates how biological complexity can interact with physical drivers and changing climates to influence R_S in ways currently unaccounted for in models.

Key words: Plant functional diversity; Soil respiration; Soil moisture; Altered precipitation; Climate change; Carbon cycle; Grassland.

HIGHLIGHTS

- Grass diversity enhanced R_S under elevated precipitation through enhanced R_H.
- Interactions between soil moisture and plant community composition changed R_S.
- Divergent R_S responses to altered precipitation arose relatively rapidly.

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INTRODUCTION

Soil respiration (R_S) is the largest contributor to the land–atmosphere carbon (C) flux, yet represents the largest source of uncertainty in those estimates (Bond-Lamberty and others 2024). Large uncertainties in model projections of R_S may arise from complexities associated with biological communities (for example, community composition and temporal dynamics) and their responses to changing precipitation, which are difficult to incorporate into models (Friedlingstein and others 2014). Over the next century, the amount and timing of precipitation is anticipated to change, which can affect the distribution and productivity of plant communities (Zeppel and others 2014). While we know less about how plant community composition changes with altered precipitation (Byrne and others 2017) than plant productivity (Knapp and others 2015), evidence suggests that when the dominant species is sensitive to altered precipitation shifts in composition can occur (Byrne and others 2017). To narrow uncertainties projecting land–atmosphere C fluxes, it is thus critical to better understand the dependence of R_S on altered precipitation, plant communities, and their potential interactions.

R_S has well established physical drivers, with soil moisture and temperature among the most well-documented (Yiqi and Zhou 2010; Manzoni and others 2012; Wang and others 2019), but both tend to operate on a local scale. On a global scale moisture and temperature alone are limited in their ability to predict R_S (Hursh and others 2017). Difficulties scaling R_S from soil moisture and temperature broadly may arise from our lack of knowledge regarding how plants influence relationships between temperature, moisture, and R_S. For example, deep rooted plants may increase soil moisture locally through hydraulic lift, increasing soil moisture in upper horizons and altering production above (Pang and others 2013) and potentially belowground, a process associated with legumes in tallgrass prairies (Horton and Hart 1998; Pang and others 2013). Metrics such as precipitation and evapotranspiration might not fully capture these phenomena.

R_S measured in situ is the sum of respiration from plant roots (R_R) and soil microbial communities (R_H) (Chen and others 2014; Jian and others 2022; Bond-Lamberty and others 2024). R_R often correlates with photosynthetic activities and root biomass (Pregitzer and others 2008; Gui and others 2018), while R_H is driven by a more complex array of drivers, such as soil moisture, pH, and substrate availability (Meier and Bowman 2008; Chen and others 2016; Liu and others 2018). R_R and R_H have different implications for C cycling. R_R represents a relatively rapid turnover of recently derived C, as roots are metabolizing photosynthates from shoots or materials stored within plant root systems. R_H, by contrast, could represent a loss of recently produced or relatively old C. Root exudation can stimulate microbial mineralization of exudates (de Vries and others 2019; Williams and de Vries 2020), representing a rapid turnover of recently fixed C. However, microbes can likewise oxidize relatively old materials, thus destabilizing stored soil C (Yin and others 2014; Zhu and others 2014). Root exudates, and root inputs generally, can become stable forms of soil organic carbon (SOC) (Iversen and others 2012; Chang and others 2024). Microbial activities can also have a stabilizing effect on soil C as their necromass appears to be one component making up relatively stable SOC forms (Liang and others 2019; Bai and Cotrufo 2022). Thus, while R_R releases recently fixed C back to the atmosphere, R_H can result in dynamic C cycle and climate feedbacks, potentially generating positive feedbacks to warming by liberating stored SOC as CO_2, or negative feedbacks to warming by generating relatively stable forms of SOC (Buckeridge and others 2022). Whether R_S is better correlated with roots or microbes thus has important implications net CO_2 loss from terrestrial ecosystems and climate feedbacks.

Whether plant diversity, community composition, or both are drivers of R_S and the direction of those relationships have been inconsistently demonstrated (Johnson and others 2008; Dias and others 2010; Chen and Chen 2019). In some instances, plant diversity is positively associated with R_S, with enhanced biomass accounting for these patterns aboveground (Zak and others 2003; Dias and others 2010) and belowground (Wang and others 2017). Alternatively, the dominant plant functional group may better predict R_S (Johnson and others 2008), which could be associate with the diversity of plant tissue chemical traits (Meier and Bowman 2008). Plants likewise provide substrate directly to rhizosphere microbes through root exudation (de Vries and others 2019; Williams and de Vries 2020), potentially stimulating R_H (Zhu and others 2014; de Vries and others 2019) and SOC decomposition (Shahzad and others 2018). While it is uncertain whether richness alone or simply the presence of a plant functional group might predict R_S, these studies suggest that accounting for plant functional type may improve our understanding of R_S.

Because R_S represents a large source of uncertainty in predicting terrestrial C losses (Bond-Lamberty and others 2024) and exploring linkages between biological communities and R_S represents a promising avenue for narrowing those uncertainties, we aimed to expand our understanding of how plant communities influence R_S. We address two outstanding questions: (1) How do interactions between plant diversity, community composition, and altered precipitation affect R_S across seasons and years? (2) What is the relative strength of relationships between aboveground, root, and microbial biomass with R_S? To address these questions, we measured R_S monthly at a local scale over four growing seasons in an established rainfall and diversity manipulation experiment that offers a degree of replication typical of plant community ecology, but only rarely leveraged in ecosystem ecology. Our work helps illuminate how biological complexity in terrestrial ecosystems must be accounted for in models projecting land–atmosphere CO_2 fluxes. As we find that high-order interactions between biological, physical, and temporal predictors were commonly significant influences on R_S, we specifically aimed to tease apart primary determinants of variation across experimental treatments and years.

METHODS

Experimental Design

A grassland rainfall and diversity (RaD) manipulation was established in spring 2018 at the University of Kansas Field Station (KUFS), including 240, 2.25 m^2 plots. Diversity manipulations were planted into a common soil (USDA classification Grundy series silty clay loam), and each plot amended with 75.1 L of native prairie soil salvaged from a road expansion project (USDA classification Kenoma-Olpe complex silty loam). From three families, asters, legumes, and grasses (Asteraceae, Fabaceae, and Poaceae), commonly represented in native tallgrass prairies we selected 18 species, six from each family (Table S1). Our experimental design manipulated diversity at two levels, by altering species richness (S) and by altering plant community composition (CC). One species of grass did not establish and in 2020 was removed from the experiment: we thus present realized richness levels of 1, 2, 3, 5, and 6 species (Table S2; N = 236). We manipulated plant community composition by selecting species for diverse communities ($S \geq 2$) from a single family or from multiple families (all asters, grasses, or legumes, and species from multiple families). Precipitation was altered to 50% and 150% ambient precipitation, which we refer to as low and high levels (Table S3, Figure S1). On average, from 2020 to 2023 the 150% plots received 1248.7 mm and the 50% treatments received 581.7 mm of combined winter precipitation and growing season irrigation (Table S3). Detailed in the supporting methods and Podzikowski and others (2023).

Soil Respiration Measurements

To measure R_S, collars were placed in all 240 plots in July 2019. Respiration collars are 10 cm diameter PVC, set to a depth of approximately 5 cm with approximately 2 cm headspace (detailed in the supporting methods). R_S measurements were taken monthly throughout four growing seasons, from May to Oct in 2020–2023 using a LiCOR 8100A-soil survey system (LI-COR Biosciences, Lincoln, NE). Observations were taken for 90 s with a 10 s post purge. We split 240 measurements into three days, taking 80 measurements in the morning from two subblocks (four sets of shelters) paired by watering treatment. We took measurements the third week of every month, though we sometimes deviated from this due to inclement weather. In some cases, only two suitable days of measurement were possible, and, in rare cases (May 2021 and October 2022), we were unable to take any measurements due to persistent inclement weather.

Soil Moisture, Temperature, Root Biomass, and Microbial Biomass

Concurrent with R_S, soil moisture measurements were taken with two types of probes at two depths. Regardless of which probe we used, moisture measurements were taken adjacent to the collars. The auxiliary sensor is a Decagon GS1 soil moisture sensor (Decagon Devices, Inc., Pullman, WA) and measures soil moisture to 5 cm. Starting in 2021, we took additional soil moisture and soil temperature measurements using Field Scout TDR 150 soil moisture meter (Spectrum Technologies, Inc., Aurora, IL; standard soil setting) to a depth of 12 cm (rod length 4.8 inches). We added the second set of measurements in 2021 because we hoped to capture soil moisture measurements reflective of a greater fraction of root biomass than the 5 cm probe permits. In 2022, we only have measurements from one of the soil moisture probes at one depth for any given timepoint due to instrument malfunctions and in 2023 we only took measurements with the Field Scout Probe at 12 cm and discontinued measurements at 5 cm.

We accounted for plant biomass above- and belowground by measuring plant cover and used root biomass data published from this experiment Podzikowski and others (2023). Plant cover observations were taken monthly throughout the growing season (May–October) by assessing the vegetative cover of all planted species in all plots. These observations were taken within seven days of the R_S measurements. Detailed methods describing the quantification of root biomass may be found in Podzikowski and others (2023). Briefly, we collected two soil cores (20 cm depth) in September 2020 (1.905 cm diameter) and 2022 (2.54 cm diameter) from all 240 plots that were composited and homogenized by plot in the field. Roots were thoroughly picked from the samples, washed with DI water, dried at 70 °C, and weighed to determine root biomass, which is presented on an areal basis.

We additionally determined microbial biomass C from the 2020 and 2022 soil samples by performing a simultaneous chloroform fumigation-extraction (CFE) procedure (Fierer and Schimel 2003). Within 48 h of collection, we weighed two 5 g subsamples of homogenized field wet soils into 40-mL centrifuge tubes. We added 20 mL of 0.5 M K_2SO_4 to all samples, while to the fumigated sample, we also added 0.5 mL of chloroform. All samples were shaken on a reciprocal shaker Table at 180 rpm for four hours, centrifuged at 3000 rpm, and decanted over Whatman 1 filter paper (Whatman Inc., New Jersey, USA). We bubbled all K_2SO_4 extractions for 20 min with air to remove any remaining chloroform from the sample and stored extractants at − 20 °C for analysis. We determined extractable organic C using colorimetric analysis (Bartlett and Ross 1988) and analyzed on a Synergy HT microplate reader (Agilent Tech., California, USA). Microbial biomass C (MBC) represents the difference between the fumigated and unfumigated subsamples. We did not apply a correction factor to these values (Craig and others 2015).

Data Analysis

To test how plant diversity, community composition, and precipitation interacted to affect R_S, we fitted linear mixed effect (LME) models predicting R_S. We additionally asked how these interactions change within a growing season and over time by including terms for month and year in the model. LME models included plant richness, plant community composition, precipitation, month, and year, as well as all potential interactions between those terms as fixed effects. Positive effects of plant richness on R_S may arise from increases in plant productivity associated with diversity (Zak and others 2003). To account for this, planted cover was added to the R_S model. Similarly, precipitation effects on R_S could arise from changes in soil moisture associated with our precipitation treatment. Moisture was added to the model to probe its effects on R_S and, since moisture squared significantly improved model fits (Table S4), it was added to account for potentially limiting effects of elevated soil moisture on R_S (Yiqi and Zhou 2010). Soil temperature was not included in the model because it strongly covaried with month and year and the latter terms improved model fits (see supporting results, Table S4, Figures S2, S3) by Akaike's information criterion (AICc) model averaging (Burnham and Anderson 2004). Three random effects were included in all LME models. We included plot identity as a random effect to account for repeated sampling of individual plots. We included subblock:rain treatment as random effect in the model to account for non-independence of diversity plots within individual shelters, and we include subblock as a random effect to account for other aspects of spatial dependence. The same LME model was run for datasets including soil moisture at 5 cm (N = 2690) and 12 cm (N = 3168). Soil moisture at 12 cm compared with 5 cm soil moisture was a better predictor of R_S (discussed in supporting results) and, as such, we focus on the models including soil moisture taken at 12 cm in the main document. All analyses were performed in R v. 4.3.2 (R Core Team 2023), and information regarding the packages used may be found in the supporting methods.

Our models included all potential high-order interactions, an approach which offers important insights into complexities associated with R_S that may contribute to noise in modeling approaches. However, since interpreting higher order interactions can be challenging, we additionally explored which two-way interactions between our experimental treatments and time best describe R_S. All potential LME models including main effects and two-way interactions of plant richness, community composition, precipitation, month, and year were compared using AIC model averaging with the 'glmulti' package (Calcagno and others 2020). The suite included 2916 candidate models. The 95% confidence set, including the models that account for 95% AIC weight cumulatively, can be found in Appendix. We present the most probable model (i.e., that model exhibiting the lowest AIC (Burnham and Anderson 2004)), sequentially adding plant cover and soil moisture terms to the model to account for productivity and moisture effects on R_S for reasons described above.

Because hydraulic redistribution could influence R_S and is often associated with plants in the legume family (Horton and Hart 1998), we additionally tested the effect of plant community composition, richness, and depth (5 cm or 12 cm) on soil moisture. We fitted LME models with plant richness, plant community composition, precipitation, and depth included as fixed effects, and all potential interactions between those terms in the model. To account for the effects of seasonal and annual variation in precipitation on soil moisture, we included month, year, and month interacting with year as random effects in the model. This LME model asks how soil moisture changes generally across seasons and year. To address how soil moisture changes over time, we fitted an LME model predicting 12 cm soil moisture as a function of plant richness, precipitation, year, and all interactions as fixed effects. Month and plant community composition were included as a random effect to test for general patterns robust to variation due to these factors.

To explore the relative contribution of aboveground, root, or microbial biomass to R_S, we fitted LME models including all three drivers as covariates and used variance partitioning to explore the effect of removing each driver from the model (detailed in the supporting methods), calculating three metrics. First, we compared how the percent variation explained by each parameter changes with the removal of each R_S driver (microbial biomass, plant biomass, and soil moisture). A positive value indicates more variation is being explained by that parameter after a driver has been removed from the full R_S driver model. Second, we assessed any change in the variation in R_S explained by the model after a R_S driver was removed from the full model. The larger the value, the more explanatory power lost by removing the driver from the model. Third, we considered how much each driver covaried with other parameters by totaling the change in the variation explained for all the parameters in a model when a R_S driver is removed. A large value indicates variation explained by the removed driver can likewise be explained by other parameters still in the model.

We present the most probable model from the exploration of the relative contribution of microbial biomass, plant biomass, and soil moisture to R_S. Using AIC_c model averaging, we compared the full model with all models with all models removing microbial biomass, plant cover, root biomass, soil moisture, and moisture squared as covariates ($N = 429$). We present the likelihood of all models defining the model with the most support as the one with the lowest AIC_c, models with high support ($0 < \Delta AIC_c \leq 2$), moderate support ($2 < \Delta AIC_c \leq 4$), and models with low support ($\Delta AIC_c > 4$). Maximum likelihood (ML) estimation is used to compare LME models with different fixed effects (Mazerolle and Mazerolle 2017), while all LME models statistics are presented using restricted maximum likelihood estimation (REML) for interpretation because it presents more unbiased estimates of variances (Laird and Ware 1982; Lindstrom and Bates 1988).

RESULTS

Using LME models testing how plant diversity, community composition, and precipitation effect soil respiration (R_S), we found strong interactions among diversity treatments and altered precipitation that varied throughout the growing season and across years (Table S5). R_S significantly increased with 12 cm soil moisture (Figure S4D) and plant cover (Figure S4F), and significantly decreased with 12 cm soil moisture squared (Figure S4E), indicating the expected inverted parabolic relationship. We observed two significant four-way interactions in the model: the interaction between precipitation, community composition, richness, and month (Figure S5), as well as the interaction between richness, precipitation, month, and year (Figure S6). Similarly, in LME models that include soil moisture measured at 5 cm, significant high-order interactions were present (Table S6). The inclusion of soil moisture did not displace main or interactive effects of precipitation on R_S (Tables S5, S6). Similarly, the inclusion of plant cover, a proxy for productivity, did not displace interactions among diversity effects. These findings demonstrate that plant diversity can interact with altered precipitation to influence R_S in ways more complex than relatively simple mediation by soil moisture or plant cover.

To facilitate interpretation of complex interactions between R_S, plant diversity, and altered precipitation, we used model selection to ask which of all potential two-way interactions between our experimental treatments and time influence R_S. The most probable model from the model selection process (Table S7) demonstrated that relationships between R_S and plant richness were expressed most clearly when water was relatively abundant and in grass communities (Figures 1, S7, Table 1). In

150% precipitation treatments, R_S increased with richness (Table 1, Figure 1a, dotted lines). In communities composed of all grasses, R_S increased with richness, while in communities composed of all legumes R_S decreased with richness (Table 1, Figure 1b, dotted lines). The relationship between R_S and richness in 150% precipitation treatments was tempered when moisture terms were added to the model (Table 1, Figure 1a, solid lines), but not cover (Table 1, Figure 1a, dashed lines). Similarly, in grass communities the addition of soil moisture (Table 1, Figure 1b, solid lines) to the model mitigated the positive relationship between R_S and richness, but not cover (Table 1, Figure 1b, dashed line). Plant cover does account for the increased R_S we observed with richness generally, as a significant main effect of richness was lost with the addition of plant cover to the model (Table 1). However, interactions among altered precipitation and diversity treatments seem to be driven by changes in soil moisture that likely varies with altered precipitation, plant community composition, and richness. We thus explored how soil moisture varies with altered precipitation and plant diversity at 5 cm and 12 cm depths.

Soil moisture is contingent on plant diversity and altered precipitation, as we observed significant three-way interactions between plant richness, precipitation, and depth as well as plant richness, community composition, and depth (Figures 2, S8, Table S8). In 50% precipitation treatments soil moisture decreased with richness at both 5 and 12 cm depths (Figure 2a, b). In 150% precipitation treatments soil moisture decreased with richness at 5 cm and the relationship between richness and soil moisture was undetectable at 12 cm (Figure 2a, b). Soil moisture at both 5 and 12 cm depths increased with richness in grass communities (Figure 2c, d). In legume communities, soil moisture at 5 cm increased with richness (Figure 2c) while soil moisture at 12 cm decreased with richness (Figure 2d). While this is consistent with hydraulic lift, it is inconsistent with hydraulic lift stimulating R_S, as we observed negative relationships between R_S and richness in legume communities (Figure 1b). Differences in soil moisture at 12 cm better corresponded with R_S than measures taken at 5 cm (Tables S5, S6). Removing 5 cm soil moisture measures from models significantly improved model fits, while that was not the case for soil moisture taken at 12 cm (ΔAIC = 3.05; see Appendix for further discussion; Figures S2g, h, i, and j, S3b, c).

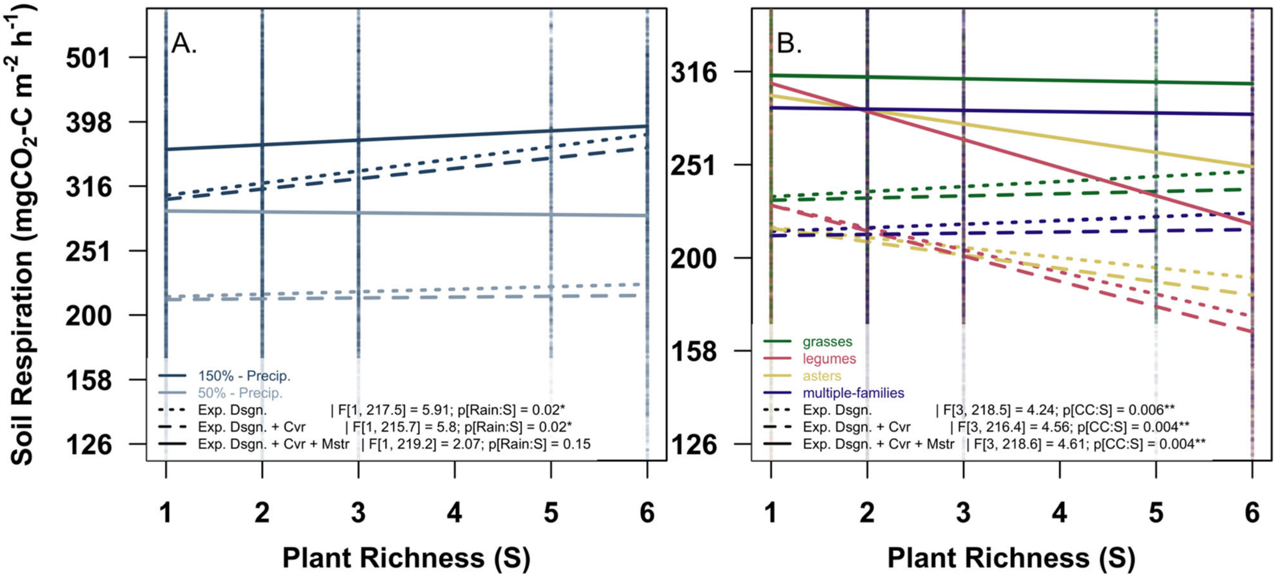

Figure 1. Effects of plant richness, precipitation, and community composition on soil respiration. Partial residual plots depicting soil respiration in **A** by plant richness and precipitation, and **B** by richness and community composition. In both panels, partial residuals are presented from the experimental design model ('Exp. Dsgn'., dotted lines), with plant cover ('Exp. Dsgn. + Cvr', dashed lines) and moisture ('Exp. Dsgn. + Cvr + Mstr'solid lines) sequentially added to the model. High and low precipitation treatments are colored in dark and light blue, respectively. Plant communities are composed of all grasses (green), legumes (rose), asters (sand), and multiple family (indigo) mixtures. Detailed model statistics can be found in Table 1. Note the difference in scales on the y-axes, which are presented at a narrow range to facilitate comparisons between slopes. The full range of data are presented in Figure S5.

Table 1. Linear Mixed Effect Model Describing Soil Respiration as a Function of Plant Diversity, Community Composition, Precipitation, and Time (Month and Year)

	Experimental Design (Exp Dsgn)	**Cover (Exp Dsgn + Cvr)**	**Cover and Soil Moisture (Exp Dsgn + Cvr + Mstr)**
Fixed effects$^{>}$	*($F_{[NumDF,\ Den,DF]}$ | Pr(> F))*		
Precipitation (Rain)	24.12 $_{[1.0,\ 4453.4]}$; 9.40e−07***	23.79 $_{[1.0,\ 4456.8]}$; 1.1e−06***	85.66 $_{[1.0,\ 2934.9]}$; 4.00e−20***
Comm. comp. (CC)	0.5957 $_{[3.0,\ 219.78]}$; 0.62	0.7225 $_{[3.0,\ 218.25]}$; 0.54	0.7214 $_{[3.0,\ 226.99]}$; 0.54
Month	39.52 $_{[5.0,\ 4454.5]}$; 7.30e−40***	39.49 $_{[5.0,\ 4513.3]}$; 7.7e−40***	64.25 $_{[5.0,\ 2958.7]}$; 7.90e−64***
Richness (S)	4.316 $_{[1.0,\ 221.84]}$; 0.039*	1.768 $_{[1.0,\ 255.90]}$; 0.18	0.2225 $_{[1.0,\ 288.57]}$; 0.64
Year	94.87 $_{[1.0,\ 4442.8]}$; 3.40e−22***	95.07 $_{[1.0,\ 4665.2]}$; 3.0e−22***	593.8 $_{[1.0,\ 3095.6]}$; 3.80e−120***
Planted cover		4.899 $_{[1.0,\ 2297.1]}$; 0.027*	25.50 $_{[1.0,\ 1386.1]}$; 5.00e−0.07***
Scale (Moisture)			286.2 $_{[1.0,\ 3084.2]}$; 1.80e−61***
Scale (Moisture^{2})			192.9 $_{[1.0,\ 3073.2]}$; 1.40e−42***
Rain:Month	66.68 $_{[5.0,\ 4461.0]}$; 2.20e−67***	62.24 $_{[5.0,\ 4459.5]}$; 6.30e−63***	12.64 $_{[5.0,\ 2929.3]}$; 3.60e−12***
CC:Month	2.488 $_{[15.0,\ 4465.0]}$; 0.0012**	2.430 $_{[15.0,\ 4458.1]}$; 0.0016**	2.309 $_{[15.0,\ 2907.2]}$; 0.0029**
Rain:S	5.918 $_{[1.0,\ 217.46]}$; 0.016*	5.803 $_{[1.0,\ 215.72]}$; 0.017*	2.073 $_{[1.0,\ 219.18]}$; 0.15
Rain:Year	24.05 $_{[1.0,\ 4453.4]}$; 9.70e−07***	23.72 $_{[1.0,\ 4456.7]}$; 1.2e−06***	85.65 $_{[1.0,\ 2934.7]}$; 4.00e−20***
CC:S	4.242 $_{[3.0,\ 218.49]}$; 0.0061**	4.565 $_{[3.0,\ 216.42]}$; 0.0040**	4.613 $_{[3.0,\ 218.61]}$; 0.0038**
Month:S	2.787 $_{[5.0,\ 4464.5]}$; 0.016*	2.921 $_{[5.0,\ 4470.5]}$; 0.012*	*2.066 $_{[5.0,\ 2922.3]}$; 0.067·*
Month:Year	39.45 $_{[5.0,\ 4454.5]}$; 8.70e−40***	39.41 $_{[5.0,\ 4513.3]}$; 9.10e−40***	68.08 $_{[4.0,\ 2972.8]}$; 3.30e−55***
Random Effects$^{>}$	*Variance (SD) | Pr(>|t|))*		
Plot	0.0047 (0.068); 2.10e−49***	0.0045 (0.067); 4.20e−46***	0.0038 (0.062); 1.30e−27***
Rain:subblock	0.00058 (0.024); 0.074·	0.00061 (0.025); 0.059·	0.00047 (0.022); 0.11
Subblock	0.00073 (0.027); 0.30	0.00067 (0.026); 0.33	0.0012 (0.035); 0.13
Residual	0.041 (0.20); NA	0.041 (0.20); NA	0.033 (0.18); NA
Marginal $r^{2>,+}$	0.404	0.406	0.534
Conditional $r^{2>,\gamma}$	0.480	0.480	0.601
df‡	51	52	53
AIC$_{c}^{‡}$	−1370.67	−1374.72	−1552.42
ΔAIC$_{c}^{‡}$	181.76	177.70	0
LL‡	736.90	739.95	830.13
AIC$_{c}$wt.‡	0	0	1

The experimental design model (Exp Dsgn) is the most probable model derived from a selection process exploring all potential two-way interactions of the experimental treatments and time as predictors of soil respiration (see Table S7 for the 95% confidence set). Plant cover (Exp Dsgn + Cvr) and soil moisture terms (Exp Dsgn + Cvr + Mstr) were sequentially added to the model. Plot, subblock, and rain nested within subblock are included in the model as random effects. The model marginal r^2, and conditional r^2 are presented for the LME model using REML estimation. To facilitate comparison among LME models with nested fixed effects, we present the model degrees of freedom (df), AIC$_c$, ΔAIC$_c$, log likelihood (LL), and model weight (AIC$_c$ wt.) for LME using ML estimation.

$^{>}$*Fixed effects, random effects, marginal, and conditional r^2 presented using REML estimation.*

$^{+}$*Variation explained by fixed effects.*

$^{\gamma}$*Variation explained by fixed and random effects.*

‡*df, AICc, ΔAIC$_c$, LL, AIC$_c$ wt. presented using ML estimation to facilitate comparison between models with nested fixed effects.*

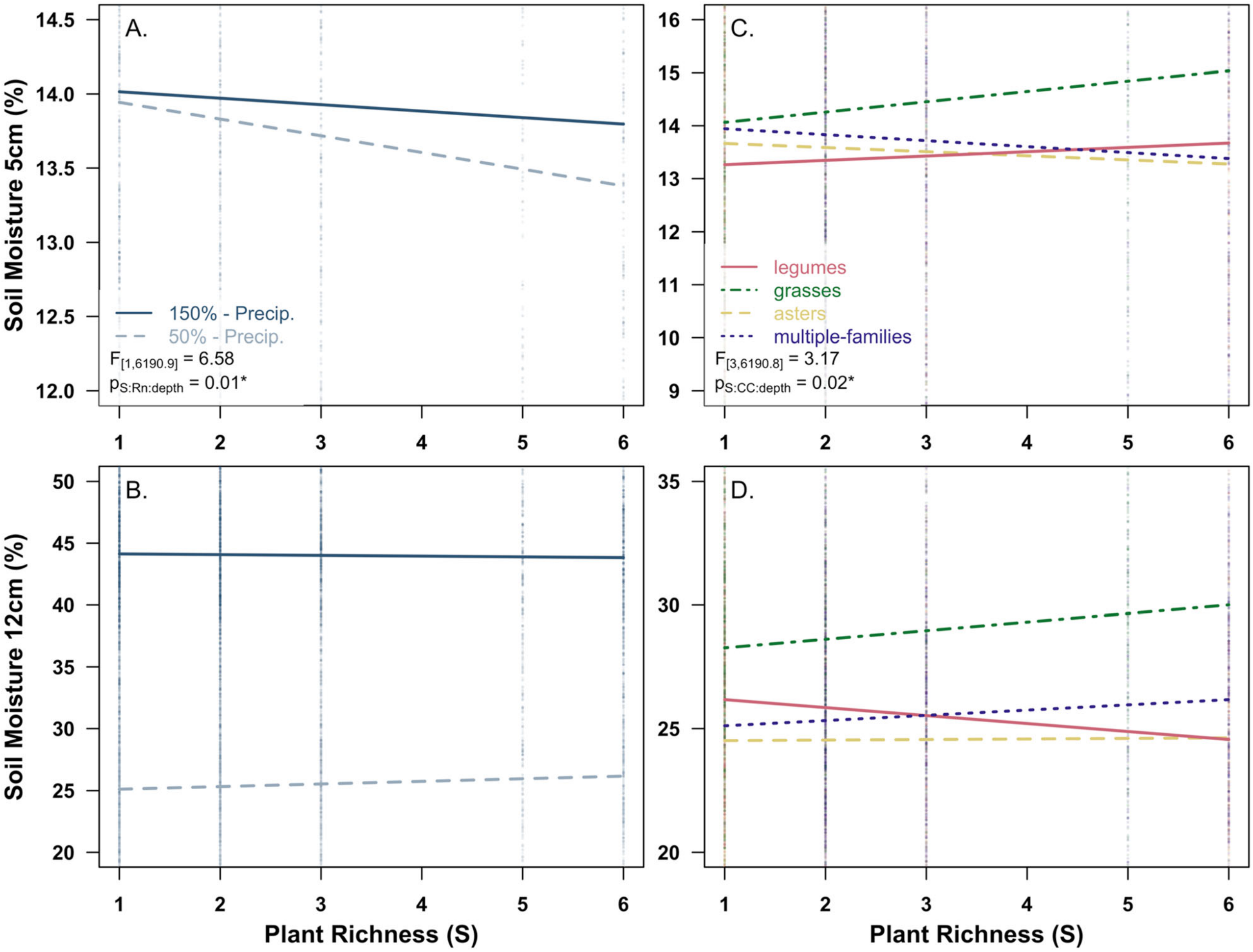

Figure 2. Effects of plant richness (S), community composition (CC), and depth on soil moisture. Partial residual plots depicting relationships between soil moisture and richness at 5 cm (panels **A** and **C**) and 12 cm (panels **B** and **D**) depths by **A**,**B**) precipitation and by **C**,**D**) plant community composition. High precipitation treatments (150%) are dark blue solid lines, and 50% precipitation are light blue dashed lines. Plant communities are composed of all grasses (green solid line), legumes (rose dot-dashed line), asters (sand dashed line), and multiple family (indigo dotted line) mixtures. Detailed model statistics can be found in Table S8. Note the difference in scales on the y-axes, which are presented at a narrow range to facilitate comparisons between slopes. The full range of data are presented in Figure S6.

Seasonality and inter-annual variation in conditions influenced the dependence of R_S on plant diversity and precipitation (Table 1, Figures 3, S9). Peak R_S occurred in July and August in year four, 2021, in both 150% and 50% precipitation treatments (Figure 3a). By year five, peak R_S shifted in 50% precipitation treatments to July, in large part because R_S rates had decreased in August and September (Figure S5). Early in the season, R_S was generally higher in 50% precipitation treatments compared with 150% treatments (Table 1; Figure 3a). Across precipitation treatments, we observed positive relationships between R_S and richness early and late in the growing season, in May, June, and October (Table 1; Figure 3b). In the middle of the growing season (July, August, and September), R_S marginally decreased with richness (Table 1; Figures 3b; S9), at times when plant biomass tended to be the greatest (Figure S10). The highest R_S rates were observed in grass communities in the middle of the season, June through September (Table 1; Figure 3c). Over time, R_S rates decreased, and the rate of decrease was greater in plots experiencing 150% precipitation compared with those receiving 50% precipitation. Plant biomass increased over time (Figure S10), which may increase demand for soil moisture, especially in high diversity plots where plant diversity had the strongest positive effect on yields. At 12 cm depths, we observed a marginal

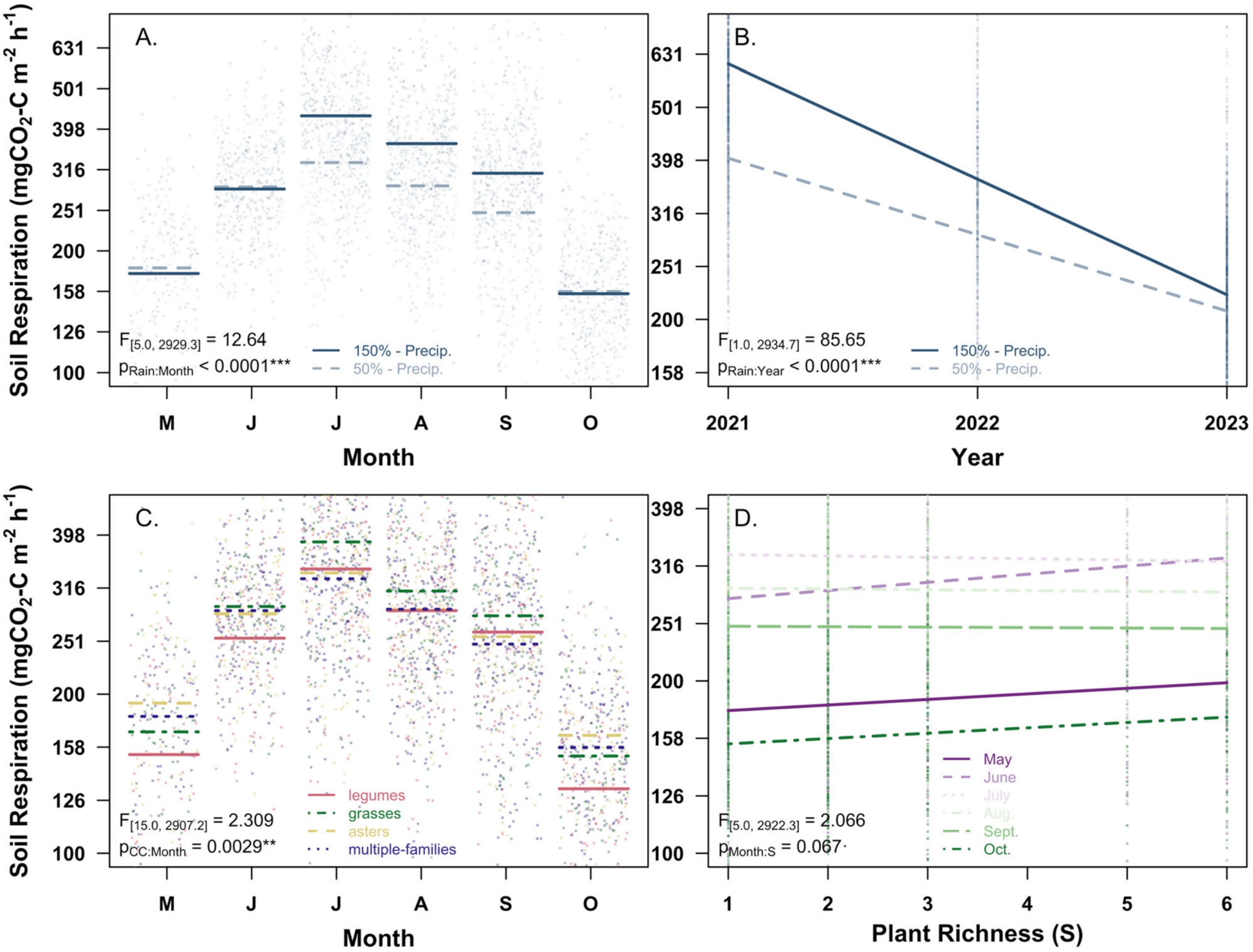

Figure 3. Effects of precipitation, plant diversity (community composition and richness), and time on soil respiration. Partial residual plots depicting soil respiration by **A** month and precipitation (Rain), **B** year and precipitation, **C** month and plant community composition (CC), and **D** species richness (S) and month. High precipitation treatments (150%) are dark blue solid lines, and 50% precipitation are light blue dashed lines. Different months are depicted in divergent purple to green colors from May–October. Plant communities are composed of all grasses (green solid line), legumes (rose dot-dashed line), asters (sand dashed line), and multiple family (indigo dotted line) mixtures. Detailed model statistics can be found in Table 1. Note the difference in scales on the y-axes, which are presented at a narrow range to facilitate comparisons between slopes. The full range of data are presented in Figure S7.

decrease in soil moisture with richness, a pattern that was consistent across time in the 150% precipitation treatments and appears to be developing over time in 50% precipitation treatments (Table S9, Figure S11).

We further tested the relative importance of biological (plant cover, root biomass, and microbial biomass) and physical (soil moisture) drivers of R_S. Since root and microbial biomass are measured less frequently and in the same month, September 2020 and 2022, temperature is not explored in this model. Microbial biomass (Figure 4a) and soil moisture (Figure 4c,d) were the strongest determinants of R_S out of the five parameters tested (Tables S10, S11). Together, microbial biomass (25%), soil moisture (25%), and moisture squared (12%) accounted for 62% of the total variation in R_S explained by predictors (Cover + Root Rmvd model). When microbial biomass was removed from the model (Microbial Biomass Rmvd: Δ var explain), the total sum of squares explained by parameters was reduced by 31%. When both moisture terms were removed from the model, the total sum of squares explained by parameters was reduced by 26% (Soil Moisture Rmvd: Δvar explain). The inclusion of terms accounting for plant cover and root biomass did not displace the effects of richness and community composition on R_S (Table S12) and surprisingly, R_S and root biomass

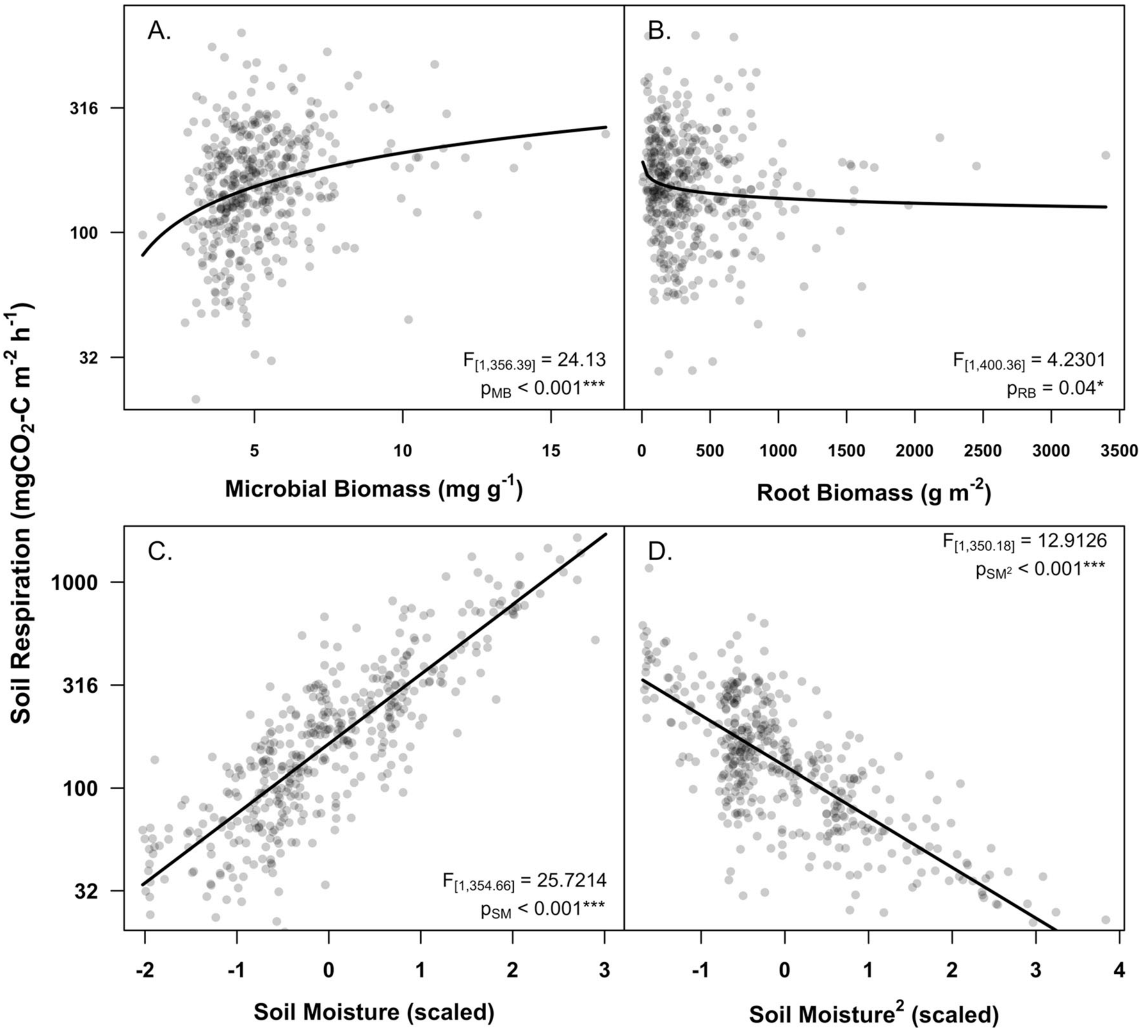

Figure 4. The relationship between soil respiration and microbial biomass, root biomass, and soil moisture. Partial residual plots depicting soil respiration as a function of **A** microbial biomass, **B** root biomass, **C** soil moisture, and **D** soil moisture squared. Since microbial and root biomass were sampled at two timepoints, this model includes soil respiration and soil moisture measurements taken in 2020 and 2022. Soil moisture and soil moisture squared are centered and scaled (standardized by subtracting the mean and dividing by the standard deviation). See Table S12 for detailed model statistics.

and R_S were negatively related (Figure 4b, Table S12).

Microbial biomass and soil moisture explained overlapping variation in R_S. When microbial biomass was removed from the model, moisture had the largest increase in the variation explained by parameters in the model, explaining 9.2% more of the variation in R_S (Table S10). Moisture squared explained an additional 4.0% of the variation in R_S, the third largest increase in variation explained after microbial biomass was removed from the model. When microbial biomass was removed from the model, soil moisture terms combined explain 13.2% more variation in R_S, representing the largest increase in variation explained by a driver when another term was removed from the model. Similarly, when both soil moisture terms were removed from the model, microbial biomass explains 13.0% more variation in R_S. This reflected the second largest increase in variation explained by an R_S driver when soil moisture was removed from the model. The overlap in variation in R_S explained by microbial biomass and soil moisture reflects meaningful covariance between those parameters, such that changes in soil moisture may indirectly account for changes in R_S by altering R_H.

DISCUSSION

The challenge of incorporating the dynamics and complexities of plant communities into predictions of terrestrial CO_2 effluxes has contributed to uncertainties in projecting C dynamics under climate change scenarios (Friedlingstein and others 2014). Our work demonstrates that interactions between soil moisture, plant diversity, and altered precipitation likely govern changes in R_S by modifying R_H. Relationships between diversity and R_S are contingent on plant community composition and are associated with interactive effects of plant diversity and community composition on soil moisture. These findings further suggest that interactions between plant communities and physical drivers of R_S cannot be captured by including physical drivers in a model as covariates. Over time, reduced precipitation shifted peaks in R_S earlier in the growing season. Generally, R_S decreased over time, which could reflect competition between plants and microbial communities for water. Soil microbial biomass emerged as the strongest independent driver of R_S, likely because R_H varied with altered soil moisture. These findings suggest interactions among soil moisture, plant diversity, and altered precipitation serve as indirect proxies for soil microbial activity directly contributing to R_S.

R_S is Contingent on Plant Community Composition

We observed increases in R_S with plant richness when communities were composed of only grasses and received elevated precipitation (Figures 1b, S5). Other studies have demonstrated that grasses can stimulate soil respiration, though this has been associated with the introduction of non-native grasses (Kumar and others 2020; Wilsey and others 2020); here we show that enhanced diversity of native grasses can similarly stimulate soil respiration. The consistent positive relationship between soil microbial biomass and soil respiration suggests that grass diversity enhances CO_2 efflux from soils by stimulating R_H rather than by enhancing R_R. Grasses may stimulate R_H indirectly by creating favorable conditions for R_H. In our experiment, grass diversity enhanced soil moisture, a pattern that was particularly true at 12 cm depths (Figure 2c,d). Increased soil moisture can increase microbial biomass (Bell and others 2014) and may indirectly stimulate R_H by mobilizing limited resources (Yiqi and Zhou 2010; Van Horn and others 2014). Grass diversity may also promote R_H through the production of root exudates. High fine root densities, a trait associated with grasses (Carmona and others 2021), is associated with high root exudation rates (Eisenhauer and others 2017), which may account for elevated R_H. Root exudation has complex implications for C cycle feedbacks. High rates of root exudation may destabilize extant soil C. Root exudates likewise may undergo stabilization via clay bonding (Bai and Cotrufo 2022), which may offset or increase soil C depending on the relative stabilization and destabilization rates. However, the stimulation of R_H by fine root exudates at the relatively shallow depths explored in the current study where organic matter, less so mineral material, dominates, seems likely.

It is unlikely that R_R contributed substantially to the relationships between richness and R_S in grass communities (Figure 4b). This finding is surprising given the high densities of fine roots produced by grasses (Carmona and others 2021), a trait which we would expect to increase R_R contributions to R_S (Wang and others 2017). However, we did not observe a positive relationship between R_S and root biomass (Figure 4b). While it is possible the timing of root sampling contributed to these findings, others suggest that R_H generates the majority ($\sim 58\%$), and R_R the minority ($\sim 42\%$), of R_S observed in the field (Jian and others 2022), which is consistent with our observations. Surprisingly, the inclusion of multiple legumes in plant communities decreased R_S (Figures 1b, S5). Legume diversity was associated with enhanced soil moisture at 5 cm and depleted moisture at 12 cm (Figure 2c, d), consistent with hydraulic lift (Horton and Hart 1998; Pang and others 2013). Hydraulic lift would be expected to enhance R_S, as favorable soil moisture conditions where soil organic material is typically more abundant should stimulate microbial decomposition (Lomander and others 1998). However, soil moisture deeper (12 cm) within soil profiles better predicted R_S. Notably soil moisture at 5 cm depths did not differ between precipitation treatments, while it did at 12 cm. These patterns likely have arisen because shallower depths are influenced more directly by evaporation (Figure S12). These patterns highlight the importance of understanding dynamics deeper within soil profiles in our attempts to draw predictive linkages between soil moisture and soil respiration.

We observe some evidence that plant biomass is linked to R_S. Previous work suggests that increased biomass associated with plant richness alone can account for positive R_S-diversity relationships (Zak and others 2003), a pattern we replicate (Table 1). We further see evidence that interactions between soil moisture and plant diversity govern R_S, with those patterns potentially influenced by plant productivity. As yields increase over time, particularly in July and August, we observed no relationship or weakly negative relationships between richness and R_S (Figure S6c,d). These patterns correspond with instances when soil moisture decreased with richness (Figure S11), suggesting that changes in soil moisture associated with higher yields may create less favorable conditions for R_S. Even after accounting for several physical and biological R_S drivers, plant community composition and richness still explained marginally significant amounts of variation in R_S (Table S12). Our findings suggest that plant community composition and richness can influence R_S through other pathways, such as soil structural changes, secondary metabolite composition, microbial community composition, and invertebrates, thus highlighting research trajectories of potential importance.

Divergent R_S Responses to Altered Precipitation Arise Over Time

By the fifth experimental year, 2022, we observed changes in R_S in high and low precipitation that differed from each other. While we could not directly compare these patterns with R_S under ambient precipitation, the most common way to test whether microbial communities are deviating from historical constraints R_S, we have two lines of evidence that suggest R_S is diverging from historical constraints. First, R_S in high and low precipitation treatments were diverging from each other over time. While the reduction in soil respiration rates over time observed in the 150% precipitation treatments may be a result of C depletion often associated with acclimation to elevated precipitation, we did not have C-poor soils (see supporting results) and, five years after establishment, we did not see differences in soil C between our precipitation treatments (Podzikowski 2023). These diverging trends indicate that our treatments are likely diverging from historical constraints. Second, we saw strong dependance of field measured R_S on both soil moisture and temperature (as indicated by month, Tables 1, S5, S6). When R_S is constrained by historical environmental conditions, field measures of soil moisture and temperature do not predict R_S.

The divergence of R_S responses to elevated and reduced precipitation may reflect changes in microbial communities in response to altered precipitation. After one growing season we observed differentiation of microbial communities in response to plant diversity (Burrill and others 2023), and after three years, differentiation due to altered precipitation (Burrill 2023). Whether ecosystems respond to altered precipitation (Preece and others 2019) or whether historical constraints limit ecosystem responses to altered precipitation (Hawkes and others 2020; Broderick and others 2022) has been inconsistently demonstrated. Why some communities overcome historical constraints and exhibit responses to changing environmental conditions while other communities do not remain uncertain. However, one explanation postulates environments experiencing relatively unpredictable fluctuations in precipitation would select for microbial communities dominated by generalists rather than specialists, which may limit ecosystem responses to change (Hawkes and others 2020). The soil amendments that we added from a mesic and undisturbed prairie facilitated the dispersal of a diverse microbial community that included locally adapted specialist taxa (Wang and others 2023). This may have contributed to the divergence R_S responses to altered precipitation that we were able to detect within a relatively short timeframe (less than five years).

CONCLUSIONS

Complex interactions between R_S and biological communities and their responses to altered precipitation will influence soil C stabilization and destabilization and thus land–atmosphere C fluxes. Microbial biomass positively predicted R_S in situ, and covariance between soil moisture and microbial biomass suggest that R_H is driving changes in R_S observed in response to altered plant community composition. Our work suggests that plant communities composed of diverse native prairie grasses may experience soil C destabilization when they experience above average precipitation, though a study of the C-balance of the system would be needed to validate those predictions. Those are the conditions grasslands in eastern North America are likely to experience under changing climates. In communities composed of a diversity of asters or plants from multiple families, plant yields increased both above and belowground (Podzikowski and others 2023), while R_S was relatively low independent of plant richness (Figure 1b). We would predict those diverse communities would be most likely to accelerate C stabilization belowground, because yields increased with richness, while R_S did not. In contrast, in diverse legume communities, root biomass does not increase with richness (Podzikowski and others 2023) and high diversity is associated with drier soils deeper in profiles, conditions that not only limit decomposition below surface soils but also the contribution of plant C to soils. In diverse legume communities, we might then speculate plant contributions to soil C would have to percolate down soil profiles from the decomposition of aboveground litter (Podzikowski and others 2024), a process that may generate C accrual belowground, but would likely occur on longer timescales relative to communities composed of a diversity of asters or plants from multiple families. Though further work is needed to link these patterns with mechanisms of soil C transformations, the importance of considering the composition of plant communities for predicting R_S is evident from our work and serves as a starting point for modelers working to project Earth's future C budgets. Our work highlights that plant traits themselves, the diversity of those plant traits, and how they influence soil moisture can directly and indirectly stimulate R_S, especially as precipitation regimes shift, a finding that illuminates the role of biological complexity in governing land–atmosphere C fluxes.

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DATA AVAILABILITY

The data and code that support this study are openly available on GitHub at < https://github.com/Lpodziko/RaDSoilRespiration2020-2023 > and on Zenodo at < https://zenodo.org/records/14217673 > .

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