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RESEARCH ARTICLE

Plant diversity increases microbial resistance to drought and soil carbon accumulation

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Abstract

1. Plant diversity is an important driver of many ecosystem functions, including decomposition and soil carbon (C) cycling. While it is well known that climate extremes can negatively impact ecosystem functions, it remains unclear how plant diversity affects soil microbial tolerance to drought and the consequences this has for soil C cycling.
2. We tested how plant diversity influences soil microbial biomass, respiration and growth under both moist conditions and during a standardised experimental drought. This was done using soils from the Jena Experiment, a long-term grassland biodiversity experiment, at two different depths (0–10 cm and 10–30 cm).
3. We found that under moist conditions higher plant diversity increased respiration rates, while microbial growth rates were stable. This may be explained by more high-quality below-ground inputs, as we found evidence for microbial use of more recently plant-derived C with increasing plant diversity. The use of organic matter containing high-quality C but low nitrogen content might have exacerbated microbial nitrogen limitation, constraining microbial growth rates. As less microbially derived organic matter was used as a source of C, this resulted in a build-up of microbial biomass that could contribute to greater soil C accumulation of microbial origin.
4. We also found a positive effect of plant diversity on microbial growth resistance to drought with increasing plant diversity. This suggests that plant diversity may have promoted drought resistance via higher availability of high-quality C that could support stress tolerance strategies.

5. *Synthesis*. Our results highlight that higher plant diversity can enhance microbial growth resistance to drought and C accumulation of both microbial and plant origin, which can strengthen soil C sequestration in grasslands.

KEYWORDS
biodiversity, climate change, Jena Experiment, microbial growth, microbial resistance, plant–soil (below-ground) interactions, respiration

1 | INTRODUCTION

Plant diversity is an important driver of many ecosystem functions (Fornara & Tilman, 2008; Hooper et al., 2012; Van Ruijven & Berendse, 2003). Higher diversity can provide more favourable conditions for soil microorganisms by stabilising temperatures and increasing resource availability through enhanced carbon (C) inputs (Eisenhauer et al., 2013; Huang et al., 2024; Mellado-Vázquez et al., 2016). Consequently, plant diversity can influence the microbial regulation of decomposition (Hooper et al., 2012), nutrient provisioning (Balvanera et al., 2006) and soil C storage (Fornara & Tilman, 2008; Lange et al., 2015), thereby linking plant and microbial functioning. However, climate extremes such as drought are increasing in frequency and intensity, posing a threat to plant–microbial systems with negative consequences for microbial functions (Chiang et al., 2021; Chomel et al., 2022; Thuiller et al., 2005; Trenberth et al., 2014).

Plant diversity can influence below-ground C via higher productivity. Higher plant productivity increases root biomass and in turn the amount of root litter and C input via root exudates (Eisenhauer et al., 2013; Mueller et al., 2013; Ravenek et al., 2014). Diverse plant communities are also more likely to contain species with different root traits that can explore larger soil volumes (Tilman et al., 2014) and reach deeper soil layers (Mueller et al., 2013). However, the increase in root biomass with plant diversity is still most pronounced in the topsoil (Ravenek et al., 2014), which suggests that plant diversity might influence microbial communities differently across soil depths (Fornara & Tilman, 2008; Lange et al., 2023). In addition, plant diversity is known to enhance microbial biomass and respiration (Eisenhauer et al., 2010; Steinauer et al., 2015; Thakur et al., 2015), as well as microbial growth, resulting in a faster microbial turnover (Prommer et al., 2020). The increase in microbial activity is likely driven by enhanced access to a higher quantity and quality of plant-derived C from rhizosphere inputs (Eisenhauer et al., 2017; Fornara & Tilman, 2008; Lange et al., 2015; Mellado-Vázquez et al., 2016), which consist of labile easily assimilable resources that microbial communities can use (Mellado-Vázquez et al., 2016; Xu et al., 2014). In turn, higher microbial growth can promote soil C accumulation by transforming C into more persistent forms, which may ultimately lead to higher soil C stocks (Bradford et al., 2013; Liang et al., 2020; Wang et al., 2021). Microbial C use efficiency (CUE), the partitioning of C between growth and respiration (Geyer et al., 2020; Manzoni et al., 2012), is also considered to be a key regulator of C storage (Tao et al., 2023). High CUE reflects greater partitioning of C to microbial biomass production, which in turn favours microbial necromass and its association with minerals, leading to stabilisation of C (Tao et al., 2023; Wang et al., 2021). While past work found CUE to be unaffected by plant diversity (Prommer et al., 2020), it is possible that, during drought, plant diversity may enhance microbial CUE by providing higher resource availability. For example, higher resource availability could support the production of osmoregulatory and extracellular polymeric substances used to resist drought (Malik et al., 2020; Schimel et al., 2007), which might help microorganisms to sustain growth and therefore result in a relatively higher CUE with plant diversity during drought.

There is growing recognition that both drought exposure and plant community composition can shape microbial communities and influence their capacity to resist drought (Bardgett & Caruso, 2020; Müller & Bahn, 2022; Oram et al., 2023). However, less is known about their interaction, especially how plant diversity affects the sensitivity of below-ground microbial communities and their functioning to drought. Observations from studies combining drought experiments with plant diversity have found contrasting effects on microbial drought resistance. Some studies have reported higher drought resistance of microbial composition and biomass with increased plant diversity (Bennett et al., 2020; Xi et al., 2023), whereas another found increased resistance of fungal community composition, but not for bacteria (Li et al., 2022). Microbial drought resistance is thought to depend on the availability of plant-derived C resources, where higher C resource availability with plant diversity can enhance the microbial ability to cope with drought (Bennett et al., 2020; Li et al., 2022; Xi et al., 2023). However, to date, no studies have assessed whether plant diversity affects the resistance of microbial growth and respiration to drought. This represents an important gap in knowledge given the importance of these microbial parameters as regulators of C cycling.

Studies have also found that more frequent drought exposure can enhance microbial drought resistance (Brangarí et al., 2021; Evans & Wallenstein, 2014). However, drought exposure varies with soil depth, as the topsoil is exposed to more frequent moisture fluctuations due to higher rates of evaporation, water uptake from roots and precipitation. As such, a higher frequency of drought exposure may select for microbial communities with higher drought resistance in the topsoil compared to deeper soil layers (Brangarí et al., 2022; Engelhardt et al., 2018). Additionally, although drought generally decreases microbial CUE due to lower substrate diffusion (Butcher et al., 2020) and higher maintenance costs (Manzoni et al., 2012), these costs might be smaller in more drought-resistant communities (Schimel et al., 2007). Given this, soil depth can be used to test the effect of differences in drought exposure on microbial processes and how this depth effect is modulated by plant diversity.

Since microbial growth and respiration play important roles in regulating soil C cycling, especially during drought, it is important to understand how plant diversity can shape these processes. To resolve this, we set out to test how plant diversity influences soil microbial functions, both under moist conditions and during a standardised drought treatment. We addressed the following two questions: first, how does plant diversity affect the microbial contribution to soil organic C accumulation, and, second, how does plant diversity alter microbial resistance to drought? To address these questions, we collected soil samples from the Jena Experiment, a long-term grassland biodiversity experiment established in 2002 that includes different plant species richness levels (1, 2, 4, 8, 16 and 60 species) and plant functional groups (small herbs, tall herbs, legumes and grasses) (Roscher et al., 2004; Weisser et al., 2017). Soil samples were collected from 80 plots at two depths (0–10 cm and 10–30 cm). A microcosm experiment was then used to assess the effect of plant diversity across soil depth on microbial growth, respiration and biomass at moist conditions, as well as microbial growth and respiration during a standardised drought treatment. We hypothesised that higher plant diversity would: (1) increase microbial biomass, growth and respiration, leading to faster turnover times and higher microbial CUE due to a higher quantity and quality of plant-derived C inputs; (2) enhance microbial drought resistance, resulting in a higher microbial CUE under the standardised drought treatment; and (3) have a stronger effect on microbial processes in the topsoil than in subsoil.

2 | MATERIALS AND METHODS

2.1 | Study site and field experimental setup

The study was carried out at the Jena Experiment field site, a long-term biodiversity grassland experiment in Jena, Germany (Roscher et al., 2004; Weisser et al., 2017). The mean annual temperature is 9.9°C and the mean annual precipitation is 610 mm (Hoffmann et al., 2014). The soil is classified as a Eutric Fluvisol (FAO-Unesco, 1997). The Jena Experiment was established in 2002, and prior to the establishment, it had been an arable field for 40 years. The field experiment consists of 80 plots, which have different plant communities with plant species richness levels of 1, 2, 4, 8, 16 and 60 species and four functional groups; small herbs, tall herbs, legumes and grasses, as described in Roscher et al. (2004). The plant species were randomly chosen from a pool of 60 mesophilic central European grassland species. The plots are arranged in four blocks with increasing distance from the Saale River to account for differences in soil characteristics, such as soil texture, pH and organic matter (Fischer et al., 2015; Roscher et al., 2004). The experimental plots are weeded two to three times a year to maintain the target plant species mixtures and are also mown twice a year, as is typical for central European hay meadows.

2.2 | Soil sampling and analysis

Soil samples were taken from 80 plots at the Jena experiment at the beginning of June 2022 using a soil corer with a diameter of 2 cm and a length of 30 cm. Four to six randomly chosen soil cores were collected from each plot and pooled together to form a composite sample. Each soil core was split into two soil depths: 0–10 cm (hereafter 'topsoil') and 10–30 cm (hereafter 'subsoil'), resulting in 160 independent samples. The samples were sieved at 4 mm and stored at 4°C until further processing. No permission was required for sampling the soil. Soil pH was measured using 10 g air-dried soil mixed with 25 mL calcium chloride solution (Orion ROSS Ultra Triode electrode). Total nitrogen (N) and total C were analysed using an Elementar Vario EL elemental analyser (Hanau, Germany). To determine the gravimetric water content, soil samples were dried overnight at 105°C. The water-holding capacity (WHC) was estimated weighing 10 g of soil into plastic tubes with an underside of nylon mesh, which was placed in water for 1 day and then allowed to drain for 6 h (Hicks et al., 2018). Data for root biomass (dataset ID 318) and aboveground plant biomass (dataset ID 579) were accessed from the JEXIS database (https://jexis.uni-jena.de/). Roots were collected and washed in 2021 from three soil cores (3.5 cm in diameter) per plot. Aboveground plant biomass was harvested in May 2022 by cutting the vegetation approximately 3 cm above the soil surface within two 20 × 50 cm frames per plot. Both roots and aboveground plant biomass were dried at 70°C for 48 h and then weighed.

The $\delta^{13}C$ signature of soil C and respired CO_2 can indicate whether the source of C is more recently plant-derived (more ^{13}C depleted) or more microbially processed (more ^{13}C enriched) (Ågren et al., 1996). The $\delta^{13}C$ signature of soil C and respired CO_2 was determined in relation to the Vienna Pee Dee Belemnite (VPDB):

$$\delta^{13}C\,(‰) = \left(\left(R_{sample} / R_{std} - 1\right) \times 1000\right) \tag{1}$$

where R_{sample} is the $^{13}C/^{12}C$ ratio of the sample and R_{std} is the $^{13}C/^{12}C$ ratio in the VPDB standard. The soil samples were air-dried prior to analysis, and the $\delta^{13}C$-SOC was measured with an IRMS using an Elemental analyser Isolink coupled to a ThermoFischer Delta V IRMS. Respired CO_2 (see Section 2.5) was sampled using a gas-tight syringe and collected in N_2-purged vials, after which the $\delta^{13}C$-CO_2 was assessed using a GasBench II coupled to a Thermo Finnigan Delta Plus XL IRMS. The respired $\delta^{13}C$-CO_2 was corrected for the background $\delta^{13}C$-CO_2 signal according to standard procedures.

2.3 | Microbial processes and drought resistance experiment

Soil subsamples were used to determine microbial biomass based on substrate-induced respiration measurements (see Section 2.5), and phospholipid fatty acid (PLFA) and neutral lipid fatty acid (NLFA) concentrations (see Section 2.4). At the start of the experiment, 150 g of soil was weighed into microcosms, adjusted to 50% WHC (optimum moisture) and kept in the dark to stabilise for 5 days. Three subsamples of each soil were kept at 50% WHC and measured as technical replicates during this initial period to characterise respiration, fungal growth and bacterial growth (see Section 2.5) under moist conditions. Based on this, microbial CUE and microbial turnover times under moist conditions were calculated (see Section 2.6).

To determine microbial drought resistance, soil samples were exposed to a standardised drought treatment under controlled conditions. To do so, the soils were gradually dried in microcosms under a ventilator at room temperature during 5 days until the soil reached air-dried conditions (~1.6% gravimetric water content; approximately −3.0 MPa water potential). During drying, soil subsamples were taken at several soil moisture levels to determine respiration, microbial growth and soil water content, and for calculating microbial CUE. A total of 12 subsamples were collected at different moisture levels per soil and measurement type (see Section 2.5).

2.4 | Phospholipid fatty acid (PLFA) and neutral lipid fatty acid (NLFA)

The PLFA composition was measured using freeze-dried samples as described by Frostegård et al. (1993) with modifications by Cruz-Paredes et al. (2017). The PLFA markers chosen for bacterial biomass were i14:0, i15:0, a15:0, i16:0, 16:1ω5c, 16:1ω7c, 10Me16:0, i17:0, a17:0, 17:1ω8, cy17:0, 10Me17:0, 18:1ω7, 10Me18:0 and cy19:0. The marker 18:2ω6, 9 was used to indicate fungal biomass and the NLFA marker 16:1ω5c was used to indicate arbuscular mycorrhizal fungi. An internal standard of 19:0 was used for quantification of fatty acid concentrations. Bacterial and fungal PLFA markers were used to estimate bacterial and fungal biomass separately (μg C g^{-1} dry soil) according to Frostegård and Bååth (1996).

2.5 | Microbial biomass, growth and respiration

Microbial biomass was assessed via substrate-induced respiration using O_2-microcompensation apparatus by adding glucose and measuring the oxygen consumption (Eisenhauer et al., 2010; Strecker et al., 2016) based on the method of Anderson and Domsch (1978). The mean of the lowest three readings within the first 10 h was taken as the maximum initial respiratory response (MIRR; μL O_2 $h^{-1}g^{-1}$ dry soil) and the microbial biomass (μg C g^{-1} dry soil) was calculated as 38 × MIRR (Beck et al., 1997).

Microbial growth was estimated as the total bacterial and fungal growth using the incorporation of radiolabelled tracers and can capture growth rates occurring in the sample prior to the preparation (Bååth et al., 2001). Bacterial growth (μg C g^{-1} dry soil h^{-1}) was determined using ^{3}H-leucine (Bååth et al., 2001). To do so, 20 mL water was mixed with 1.0 g of soil. Leucine solution with a concentration of 275 nM was added to 1.5 mL of bacterial suspension and then incubated at 19°C. Bacterial growth was terminated after 1 h using 75 μL trichloroacetic acid. The incorporated leucine was extracted as described in Bååth et al. (2001). To determine bacterial growth rates in C units, a conversion factor between thymidine and leucine was determined using ^{3}H-thymidine in the moist control samples kept at 50% WHC (Soares & Rousk, 2019; Tang et al., 2023). Fungal growth (μg C g^{-1} dry soil h^{-1}) was determined using ^{14}C-acetate into ergosterol (Bååth, 2001; Rousk et al., 2009). To do so, 2 mL acetate solution with a concentration of 220 μM was added to 1.0 g of soil. The samples were incubated at 19°C. Fungal growth was terminated after 2 h using 500 μL 10% formalin. Ergosterol was extracted and separated as described in Rousk and Bååth (2007). The fungal growth was converted to C units according to Soares and Rousk (2019).

The soil respiration rate (μg C g^{-1} dry soil h^{-1}) was estimated as the CO_2 production in 20 mL headspace vials using 1.0 g of soil. The soil samples were incubated for 24 h, after which the amount of accumulated CO_2 was analysed using gas chromatography with a thermal conductivity detector.

2.6 | Data analysis and statistics

The mean value for the three technical replicates kept at 50% WHC was used for further analysis of microbial growth, respiration, CUE and microbial turnover time under moist conditions. The CUE was estimated as the C used for microbial growth per total C use (Manzoni et al., 2012; Soares & Rousk, 2019).

$$\text{CUE} = \frac{\text{microbial growth}}{\text{microbial growth} + \text{respiration}} \tag{2}$$

The microbial turnover time was estimated as microbial biomass (based on the total PLFA biomass) divided by the microbial growth rate. The microbial C availability was assessed as the total microbial C use (respiration + microbial growth) per total soil C.

Microbial communities with higher drought resistance are able to maintain activity at lower soil moisture (Griffiths & Philippot, 2013). To determine microbial drought resistance, logistic curves (Equation 3) were fitted to the microbial activity (growth or respiration) measured at several different soil moisture levels (see Section 2.3) for each soil sample using Kaleidagraph 4.5 (Synergy Software).

$$y = \frac{c}{1 + e^{b(x-a)}} \tag{3}$$

where *y* is the rate of microbial growth or respiration, *x* is the soil moisture expressed as % WHC, *a* is the soil moisture when microbial growth or respiration is inhibited by 50% (i.e. IC_{50}), *b* is a fitted parameter indicating the inhibition rate, and *c* is the maximum growth or respiration rate in one soil sample. For some replicates, double logistic curves were fitted to represent the data better, as described in Rath et al. (2019). The curves for each soil sample for microbial growth and respiration were normalised by the maximum growth or respiration rate *c*, and the curves were then refitted to assess the IC_{50} values, that is the soil moisture (% WHC) when the microbial growth or respiration rate was inhibited by 50%. The IC_{50} value was used as an estimate for drought resistance for microbial growth and respiration in each replicate, where lower IC_{50} values indicate higher drought resistance and higher IC_{50} values indicate lower drought resistance (Tang et al., 2023).

Statistical analyses were performed using R v. 4.3.1 (R Core Team). To test the effects of plant species richness (hereafter 'plant diversity') and functional groups on all measured response variables (field and soil characteristics, microbial biomass, growth, respiration, turnover, CUE and drought resistance), we used a linear mixed effects model with type I sum of squares. The linear mixed model was performed using the nlme package (Pinheiro et al., 2024). Block was included as a random factor, and plant diversity (log 2-transformed), functional group and soil depth as fixed factors and soil depth as an interaction with plant diversity and functional group. The full statistics of the linear mixed effects models are found in Table S1. All response variables were also tested separately for each soil depth using linear mixed models with block as a random factor and plant diversity (log 2) and functional group as fixed factors. The PLFA composition was analysed with principal component analysis (PCA) using the vegan package (Oksanen et al., 2013).

3 | RESULTS

3.1 | Soil and field characteristics

Soil characteristics were influenced by both plant diversity and soil depth (Table 1). Total soil C ($p < 0.001$) and N ($p < 0.001$) both increased with higher plant diversity, with lower values in the subsoil. The increase in total C and N from monocultures to 60 species mixtures was larger in the topsoil (21% and 37%, respectively) compared to the subsoil (6% and 16%, respectively) (plant diversity × soil depth interaction effect: $p < 0.001$). The lower relative increase of total C in the subsoil resulted in a non-significant relationship with plant diversity when tested separately ($p = 0.20$). The C/N ratio decreased with increasing plant diversity ($p < 0.001$), with higher values in the subsoil compared to the topsoil ($p < 0.001$).

In plots with higher plant diversity, microbial C availability increased ($p = 0.004$; Table 1) and was higher in the topsoil than in the subsoil ($p < 0.001$). Both the $\delta^{13}C$-respired CO_2 ($p = 0.04$) and $\delta^{13}C$-SOC ($p = 0.001$) were more ^{13}C-depleted in the topsoil with increasing plant diversity, but there was no relationship with plant diversity in the subsoil ($p = 0.97$ and $p = 0.42$, respectively; Table 1).

TABLE 1 Summary of soil and plant characteristics at each plant species treatment in the topsoil (0–10 cm) and the subsoil (10–30 cm), values show mean ± SE[a].

Plant diversity	TC (%)	TN (%)	C/N ratio	$\delta^{13}C-CO_2$	$\delta^{13}C$-SOC	C availability index (µg C g^{-1} SOC h^{-1})	Soil pH	Root biomass (g/m^2)
Topsoil (0–10 cm)								
1	3.7 ± 0.3	0.21 ± 0.01	18.0 ± 1.6	−27.5 ± 0.5	−18.1 ± 1.5	33 ± 3	7.41 ± 0.01	130 ± 30
2	3.9 ± 0.3	0.23 ± 0.01	17.5 ± 1.4	−28.6 ± 0.8	−18.2 ± 1.1	36 ± 3	7.38 ± 0.01	110 ± 20
4	4.0 ± 0.3	0.25 ± 0.01	16.4 ± 1.1	−29.3 ± 0.8	−18.5 ± 1.1	40 ± 4	7.37 ± 0.01	230 ± 50
8	4.0 ± 0.3	0.24 ± 0.01	16.8 ± 1.0	−28.6 ± 0.9	−19.1 ± 1.1	46 ± 6	7.34 ± 0.01	300 ± 50
16	4.2 ± 0.3	0.27 ± 0.01	15.9 ± 1.1	−29.7 ± 0.9	−19.8 ± 1.1	38 ± 3	7.34 ± 0.01	260 ± 30
60	4.5 ± 0.5	0.29 ± 0.01	15.8 ± 1.8	−30.9 ± 0.6	−20.0 ± 2.0	46 ± 7	7.30 ± 0.03	390 ± 130
Subsoil (10–30 cm)								
1	3.4 ± 0.2	0.18 ± 0.01	20.1 ± 2.2	−27.2 ± 1.0	−16.4 ± 1.1	23 ± 2	7.44 ± 0.02	100 ± 20
2	3.6 ± 0.3	0.18 ± 0.01	20.5 ± 2.3	−28.6 ± 0.8	−15.6 ± 1.3	26 ± 2	7.45 ± 0.02	110 ± 20
4	3.6 ± 0.2	0.19 ± 0.01	19.2 ± 1.7	−27.2 ± 1.2	−17.5 ± 1.3	22 ± 2	7.44 ± 0.02	200 ± 50
8	3.5 ± 0.2	0.18 ± 0.01	19.2 ± 1.6	−28.1 ± 0.8	−18.7 ± 1.3	27 ± 2	7.42 ± 0.02	180 ± 30
16	3.6 ± 0.3	0.20 ± 0.01	18.1 ± 1.5	−26.7 ± 0.9	−16.8 ± 1.1	25 ± 2	7.43 ± 0.02	210 ± 40
60	3.7 ± 0.4	0.20 ± 0.00	18.4 ± 2.2	−28.7 ± 1.5	−16.4 ± 2.1	30 ± 8	7.37 ± 0.04	210 ± 30

[a] Total carbon (TC), total nitrogen (TN), carbon to nitrogen ratio (C/N ratio), $\delta^{13}C-CO_2$ respired as CO_2 and $\delta^{13}C$-SOC in the soil C.

In addition, the δ^{13}C-respired CO_2 was consistently lower (i.e. more ^{13}C depleted) than the δ^{13}C-SOC (Figure S1).

The microbial community composition based on PLFA markers differed with soil depth and plant diversity (Figure S2), where PC1 explained 20% and PC2 explained 16% of the variation. The PC1 axis was positively correlated with plant diversity ($p = 0.001$; Figure S3).

Soil pH was close to neutral with a mean value of 7.4 which decreased slightly, albeit significantly, with increasing plant diversity ($p < 0.001$) and soil depth ($p < 0.001$). There was no difference in soil gravimetric water content at the time of sampling among plant diversity treatments ($p = 0.13$), with soil moisture being ~22% WHC. Root biomass increased with plant diversity ($p < 0.001$), with a threefold increase in the topsoil and a twofold increase in the subsoil. In addition, the root biomass in monocultures was similar at both soil depths, but in the 60 species plant mixtures it was 52% higher in the topsoil than in the subsoil ($p = 0.02$). Plant aboveground biomass also increased with plant diversity ($p < 0.001$).

3.2 | Plant diversity effects on microbial C processes

At moist conditions, microbial growth did not show any relationship with plant diversity ($p = 0.82$; Figure 1a), whereas respiration was positively affected by plant diversity ($p < 0.001$; Figure 1b). This was observed at both soil depths, with respiration being 83% greater in the topsoil and 59% higher in the subsoil at 60 plant species mixtures than in monocultures ($p = 0.01$). Both microbial growth and respiration were higher in the topsoil compared to the subsoil ($p < 0.001$ and $p < 0.001$, respectively). Microbial CUE was negatively affected by higher plant diversity ($p < 0.001$; Figure 1c) and was approximately 30% higher in the subsoil compared to the topsoil across all diversity treatments. The fungal to bacterial growth ratio increased with higher plant diversity ($p = 0.01$; Figure 1d), but did not differ significantly between soil depths ($p = 0.13$).

Plant diversity had a positive effect on microbial biomass ($p < 0.001$), and the biomass was greater in the topsoil than in the subsoil ($p < 0.001$; Figure 2a). The plant diversity-induced increase in microbial biomass was more pronounced in the topsoil, 58%, compared to the subsoil, 48% ($p = 0.01$). A similar trend was also observed for bacterial, fungal and arbuscular mycorrhiza fungal biomass (Figure S4). While the fungal-to-bacterial biomass ratio did not show a consistent pattern across plant diversity treatments ($p = 0.11$), it was significantly higher in the topsoil ($p < 0.001$; Figure 2b). Plant diversity increased microbial turnover time ($p < 0.001$; Figure 3). Specific turnover times for bacteria and fungi were also slower with increasing plant diversity (Figure S5), with a more pronounced effect for bacteria (60%) compared to fungi (35%) between monocultures and 60 species mixtures.

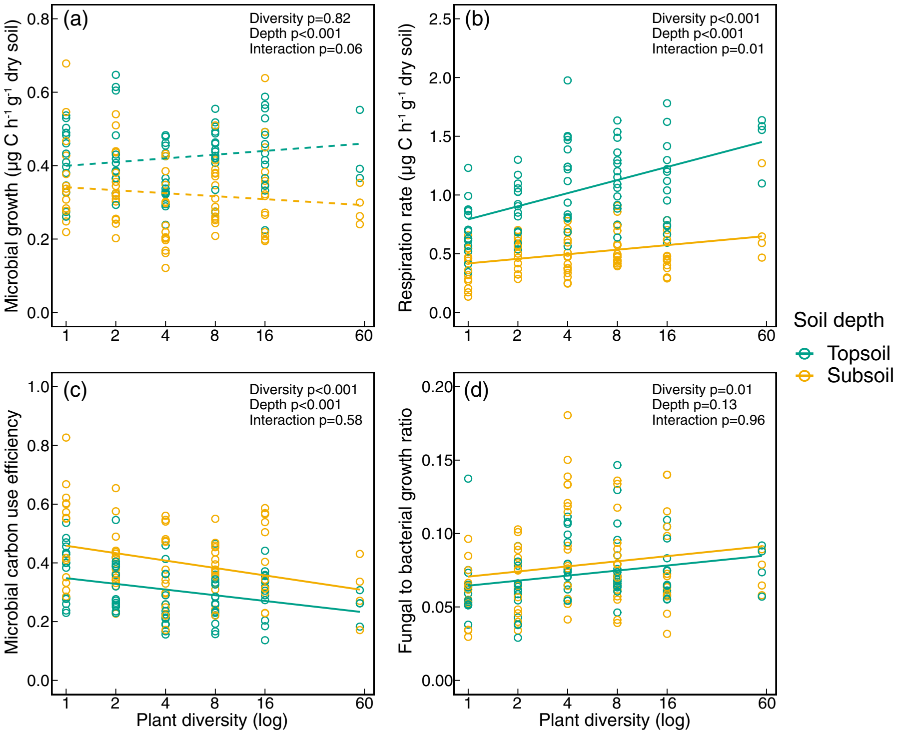

FIGURE 1 Effects of plant diversity measured at moist conditions (50% WHC) on (a) microbial growth, (b) respiration, (c) microbial carbon use efficiency and (d) fungal-to-bacterial growth ratio. Green colour represents the topsoil (0–10 cm) and the orange colour represents the subsoil (10–30 cm). Significant plant diversity effects are indicated by solid lines, while non-significant effects are indicated by dashed lines.

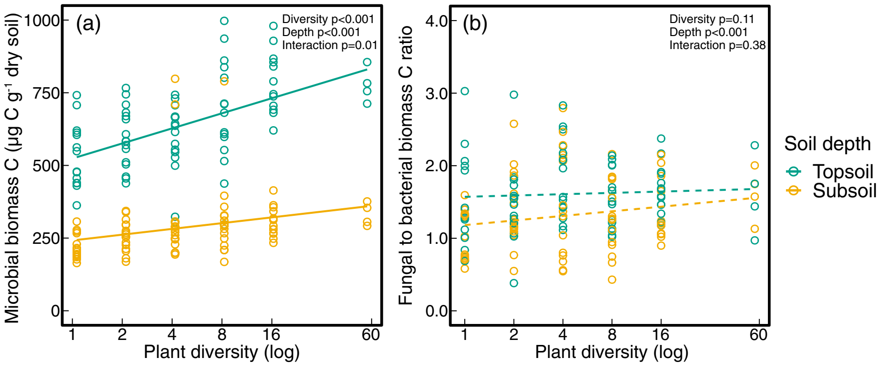

FIGURE 2 Effects of plant diversity on (a) microbial biomass and (b) fungal-to-bacterial biomass ratio. Green colour represents the topsoil (0–10 cm) and the orange colour represents the subsoil (10–30 cm). Significant plant diversity effects are indicated by solid lines, while non-significant effects are indicated with dashed lines.

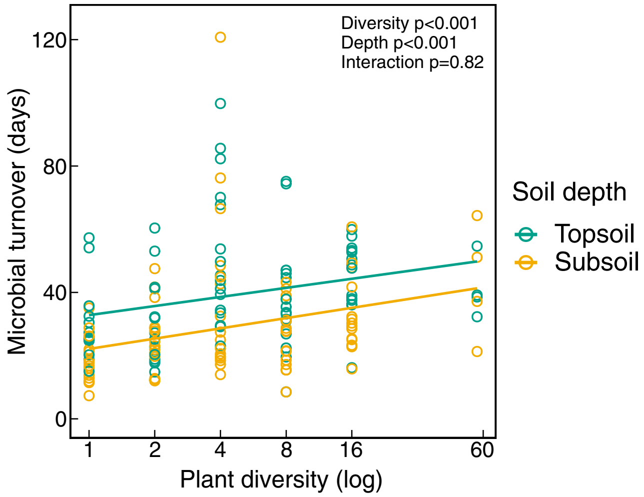

FIGURE 3 Soil microbial turnover time affected by plant diversity in two soil depths. The green colour represents the topsoil (0–10 cm) and the orange colour represents the subsoil (10–30 cm).

3.3 | Effect of plant diversity on microbial drought resistance

Microbial growth and respiration rates decreased with lower soil moisture (Figure 4a,b). Plant diversity had a positive effect on microbial growth resistance to drought ($p = 0.008$; Figure 4c) and was higher in the topsoil ($p < 0.001$). Microbial growth resistance to drought increased by 15% in soils from both depths between the lowest and highest plant diversity mixtures. Generally, respiration showed lower resistance than growth (Figure 4d), as indicated by higher IC_{50} values (20.6 ± 0.6% and 13.9 ± 0.3% WHC, respectively). In contrast to microbial growth, the resistance of respiration to drought was unaffected by plant diversity ($p = 0.46$) but was consistently higher in the subsoil ($p = 0.01$). In general, fungal growth showed a higher drought resistance than bacterial growth (IC_{50} of 6.3 ± 0.4% and 14.3 ± 0.4% WHC, respectively). Plant diversity had a positive effect on bacterial growth resistance to drought ($p = 0.003$), and the bacterial growth resistance was also higher in the topsoil ($p < 0.001$), whereas fungal growth resistance was unaffected by both plant diversity ($p = 0.18$) and soil depth ($p = 0.17$; Figure S6).

4 | DISCUSSION

4.1 | Higher microbial respiration but not growth with increasing plant diversity

Plant diversity is an important driver of microbial-mediated soil functions, via higher below-ground C inputs with increasing plant diversity (Fornara & Tilman, 2008; Hooper et al., 2012; Xu et al., 2020). In the Jena experiment, previous studies have reported a positive relationship between plant diversity and microbial respiration (Eisenhauer et al., 2010; Lange et al., 2015) and microbial growth (Prommer et al., 2020). Based on these findings, we expected microbial rates measured under moist conditions to increase with higher plant diversity. Our results confirmed an increase in microbial respiration with higher plant diversity (Figure 1); however, microbial growth was not affected. What can cause these contrasting responses of respiration and growth?

Higher plant diversity is usually associated with increased microbial access to high-quality C rhizosphere inputs, which microorganisms can easily use (Mellado-Vázquez et al., 2016; Steinauer et al., 2016). As such, microbial communities might selectively use more recent plant-derived C over more microbially processed C, as the latter is of lower C quality (Kuzyakov, 2002; Rousk & Frey, 2015). Indeed, the more depleted $\delta^{13}C$ signature in respired CO_2 at higher plant diversity in the topsoil (Table 1) suggests a microbial preference for more recent plant-derived C. This interpretation is further reinforced by more ^{13}C-depleted respiration compared to that in the soil C (Figure S1), indicating a general microbial preference for plant-derived C relative to the averagely available soil C. Below-ground rhizosphere inputs are rich in high-quality C but low in N compared to organic matter of microbial origin (Hirsch et al., 2013). Thus, microbial communities using more plant-derived inputs might become relatively more N-limited, potentially influencing growth

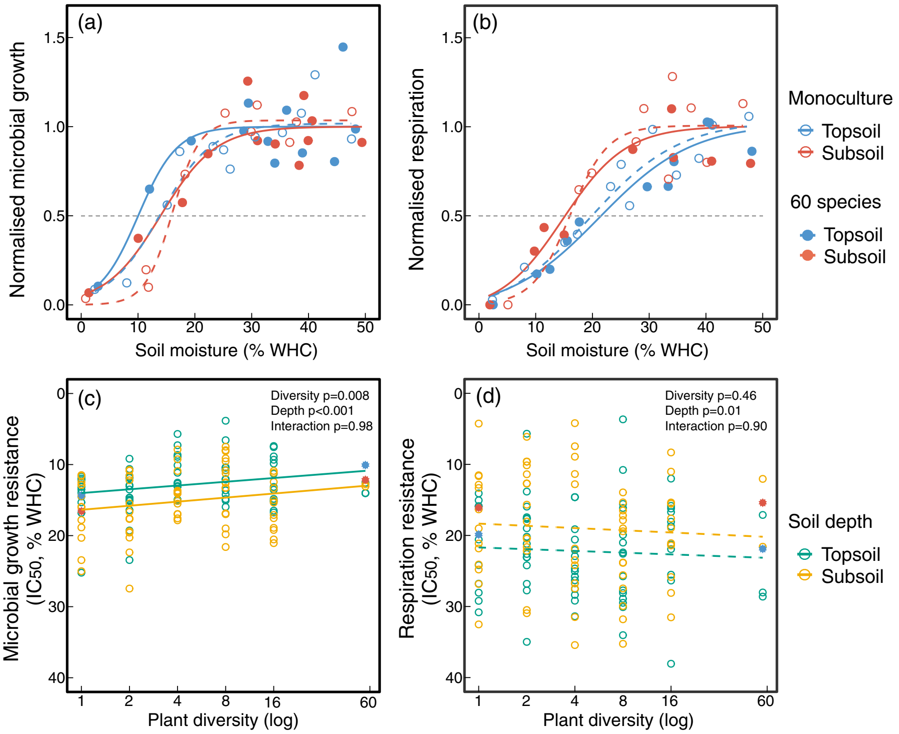

FIGURE 4 Normalised respiration and microbial growth rates at different soil moisture levels during the experimental drought treatment for (a) monoculture treatment and (b) 60-plant species treatment. The blue colour represents the topsoil (0–10 cm) and the red colour represents the subsoil (10–30 cm). Filled circles show the 60 species treatment and empty circles show the monoculture. The drought resistance (i.e. IC50) was estimated as the soil moisture when the rate of respiration or growth was reduced by 50%, showed by grey dashed line. The effects of plant diversity on (c) microbial growth resistance to drought and (d) respiration resistance to drought. Green colour represents the topsoil (0–10 cm) and the orange colour represents the subsoil (10–30 cm). Significant plant diversity effects are indicated by solid lines, while non-significant effects are given with dashed lines. Stars in red and blue represent the selected curves in (a) and (b).

and respiration differently. Here we propose that lower biological N-availability at higher plant diversity is mediated by a preferential microbial use of easily available C, leading to unchanged growth but excess respiration. These contrasting results compared to Prommer et al. (2020), who found a positive effect on growth with plant diversity, might be because their soils were sampled 7 years earlier, thus reflecting differences in nutrient limitation over time. Consistent with this, during the first years of the Jena Experiment, microbial communities were found to be more N-limited in monocultures than at high plant diversity treatments (Eisenhauer et al., 2010). However, soil N-availability has decreased since the beginning of the experiment and N has also become less available with increasing plant diversity (Guiz et al., 2016). Even though total N increased with higher plant diversity, resulting in a lower soil C/N ratio (Table 1), this N might not be available to microorganisms, as it might be in forms that are inaccessible, such as those protected within soil aggregates, bound to mineral surfaces or contained in living biomass.

4.2 | Microbial contribution to soil C accumulation

Higher plant diversity may lead to higher soil C via increased plant productivity and below-ground root biomass (Fornara & Tilman, 2008; Steinbeiss et al., 2008). As such, the observed increase in soil C with plant diversity (Table 1) may be attributed to both higher root C inputs to the soil and by microbial growth that can transform labile C into more persistent forms of organic matter (Lange et al., 2015, 2023; Mellado-Vázquez et al., 2016). Plant diversity has often been shown to have a positive effect on microbial biomass, mediated by higher quality resources (Eisenhauer et al., 2010, 2017; Lange et al., 2023; Steinauer et al., 2015; Thakur et al., 2015; Zak et al., 2003). In line with this, we also found higher microbial biomass with increased plant diversity (Figure 2), which was in accordance with our hypothesis. The higher microbial biomass might be a result of a lower use of microbially processed C, that is necromass in favour of plant-derived C, as indicated by the more depleted $\delta^{13}C\text{-}CO_2$ (Table 1). The lower use of microbially processed C might have resulted in slower microbial turnover times, leading to higher microbial biomass at higher plant diversity, which via growth can be transformed into more stable forms that may remain in the soil as necromass (Liang et al., 2017). This interpretation is in agreement with Lange et al. (2015, 2023), who proposed that the positive effect of plant diversity on soil C storage results from reduced decomposition of 'older' C, leading to a build-up of necromass and plant material. In addition, we found a reduced CUE with higher plant diversity (Figure 1c) likely due to microbial nutrient limitation (Manzoni et al., 2012). The C gain via microbial transformation and higher root inputs at higher diversity appeared to exceed the losses from microbial respiration, leading to accumulation of soil C. Our results provide evidence that plant diversity can promote soil C accumulation of microbial origin, which can persist in the soil. However, the higher soil C with plant diversity might also be partly attributed to more plant C inputs such as root litter (Lange et al., 2015). This idea is supported by a more depleted δ^{13}C signal in the soil at higher diversity, which indicates a higher proportion of recent plant-derived C. As such, our results indicate that both microbial processes and plant C inputs contribute to the higher total soil C at high plant diversity.

4.3 | Increased microbial growth resistance to drought with plant diversity

In line with our hypothesis, we found that higher plant diversity gave rise to higher microbial growth resistance to drought (Figure 4). The positive plant diversity effect on microbial growth resistance could be explained by several mechanisms. First, higher plant diversity can provide more favourable conditions during drought, as diverse communities are more productive, have higher root biomass and supply more root-derived inputs that act as extra resources to better withstand drought (Fornara & Tilman, 2008). For example, these plant-derived inputs may enhance microbial drought resistance by supporting osmoregulation and the production of extracellular polymeric substances to help resist desiccation (Malik et al., 2020; Schimel et al., 2007). This interpretation is supported by the more depleted δ^{13}C signature of respired CO_2 than soil C, indicating that microbial communities have access to more plant-derived C with higher plant diversity in the topsoil. Second, plant diversity resulted in changes in microbial community composition (Figure S2; Steinauer et al., 2016). Higher plant diversity also resulted in a higher fungal-to-bacteria ratio (Figure 1d), in accordance with other studies (Chen et al., 2019; De Deyn et al., 2011) and may have enhanced microbial drought resistance since fungi are generally more resistant to drought than are bacteria (de Vries et al., 2018). Another potential driver could be that more diverse ecosystems resist drought disturbances better via the insurance effect, where diverse plant communities support more diverse microbial communities increasing the likelihood of including more drought-tolerant species (Yachi & Loreau, 1999). Indeed, microbial diversity has been shown to increase with higher plant diversity (Lange et al., 2015). These combined factors suggest that more diverse plant communities may be promoting microbial growth resistance in several ways, via shifts in community composition as well as the availability of resources to cope with drought. Contrary to our hypothesis, the drought resistance of respiration was generally not affected by plant diversity. However, we showed that respiration was more sensitive than microbial growth to drought, as indicated by a faster reduction in rates with lower soil moisture (Figure 4). This is also reflected in the generally higher CUE at lower moisture levels compared to at 50% WHC across all plant diversity treatments (Figure S7). The increased CUE suggests that with future increases of drought frequency, microbial communities can shift towards more efficient use of C contributing to soil C in grasslands soils independent of plant diversity.

We also found that fungal communities were more drought resistant than bacteria, as they were able to maintain growth rates at lower levels of soil moisture (Figure S6), in accordance with previous findings (Barnard et al., 2013; Dacal et al., 2022; de Vries et al., 2012; Leizeaga et al., 2021). Fungi might be more drought resistant than bacteria due to their thicker cell walls which are likely to resist drought better (Harris, 1981) and their ability to better access water via hyphal translocation compared to bacteria (Karlowsky et al., 2018). In addition, there was no relationship between fungal resistance and plant diversity, possibly due to the generally high resistance of fungal growth. As such, the microbial growth resistance to drought was mainly driven by the sensitivity of bacterial rates across plant diversity treatments.

4.4 | Microbial responses to plant diversity were generally stronger in the topsoil

Matching our expectations, microbial growth resistance to drought was higher in the topsoil (Figure 4), suggesting that these microbial communities are better able to cope with drought. Several reasons could contribute to this higher resistance. First, the topsoil receives larger inputs of high-quality plant-derived C (Eisenhauer et al., 2010; Fornara & Tilman, 2008; Steinauer et al., 2016), which could help microbial communities to invest in strategies to mitigate stress (Brangarí et al., 2018; Schimel, 2018). This is supported by both the higher amount of total C and higher microbial C availability in the topsoil (Table 1). Second, the topsoil is more exposed to fluctuations in soil moisture due to evapotranspiration and precipitation (Engelhardt et al., 2018). Indeed, bacterial communities previously exposed to experimental summer drought (de Nijs et al., 2019) or originating from drier climates (Tang et al., 2023; Winterfeldt et al., 2024) generally show higher growth resistance to drought. Together, these lines of evidence suggest that microbial communities in the topsoil might have already shifted to a more drought-tolerant community, leading to higher growth resistance compared to those in the subsoil. This is supported by several recent dry years at the Jena Experiment (Huang et al., 2024), which might have selected for more drought-tolerant communities (Albracht et al., 2023; Delgado-Baquerizo et al., 2017; Evans & Wallenstein, 2014; Metze et al., 2023).

Root biomass exhibited a stronger increase in the topsoil with greater plant diversity compared to the subsoil (Table 1), which was consistent with other studies (Mommer et al., 2010; Mueller et al., 2013; Ravenek et al., 2014). In accordance with our expectations, we found evidence for a stronger response to plant diversity in the topsoil compared to the subsoil for both microbial respiration and biomass, as well as a tendency for growth rates. The positive plant diversity effect in the topsoil is likely caused by higher inputs of plant-derived C, as shown by the higher microbial availability of C (Table 1). While this mechanism might also apply to the subsoil, lower root biomass and microbial activity at depth result in weaker patterns that may obscure the relationships. In the subsoil, there was no detectable link between plant diversity and the $\delta^{13}C$ of respired CO_2 or SOC.

5 | CONCLUSION

Our findings indicate that higher plant diversity promotes microbial processes that contribute to greater soil C accumulation. Increased plant diversity enhances plant-derived C inputs to the soil, which can directly explain the higher SOC observed, but these inputs also support higher microbial biomass, further contributing to soil C build-up. The preferential use of easily available high-quality C at higher plant diversity led to higher respiration rates but also exacerbated microbial N limitation, resulting in unchanged microbial growth and reduced CUE. Furthermore, our results suggest that the availability of high-quality C at higher diversity supports mechanisms that enhance microbial drought resistance or by favouring more drought-tolerant microbial taxa. The higher resistance of microbial growth compared to respiration also resulted in higher CUE under low soil moisture conditions, suggesting a shift towards more efficient C use under future drier climates. Overall, our study demonstrates that higher plant diversity supports both microbial growth resistance to drought and the accumulation of microbially- and plant-derived C, thereby reinforcing the role of diverse grasslands as important soil C sinks.

AUTHOR CONTRIBUTIONS

Sara Winterfeldt, Albert C. Brangarí, Lettice C. Hicks, Nico Eisenhauer and Johannes Rousk planned and designed the experiment. Sara Winterfeldt, Albert C. Brangarí, Shangshi Liu, Nico Eisenhauer and Johannes Rousk carried out the sampling. Sara Winterfeldt and Shangshi Liu performed the experiments and analysed the data. Richard D. Bardgett, Nico Eisenhauer and Johannes Rousk acquired the funding. Sara Winterfeldt wrote the manuscript supervised by Johannes Rousk, Albert C. Brangarí and Lettice C. Hicks. All authors contributed critically to the draft and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. Richard Bardgett is an Editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70250.

DATA AVAILABILITY STATEMENT

The datasets are available in The Jena Experiment database (JEXIS: https://jexis.uni-jena.de/). PLFA and NLFA (https://doi.org/10.25829/4DA9-MH06; Winterfeldt, Brangarí, et al., 2026a) and (https://doi.org/10.25829/C5T2-QQ47; Winterfeldt, Brangarí, et al., 2026b). Microbial growth and respiration (https://doi.org/10.25829/YESW-GY64; Winterfeldt, Brangarí, et al., 2026c). $\delta^{13}C$ (https://doi.org/10.25829/ZA1R-TH28; Winterfeldt, Brangarí, et al., 2026d). Total C and N (https://doi.org/10.25829/GF6J-WM16; Winterfeldt, Liu, et al., 2026). Microbial biomass (https://doi.org/10.25829/907A-1366; Lochner et al., 2026).

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SUPPORTING INFORMATION

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

Figure S1. Relationship between respired δ^{13}C-CO$_2$ and soil δ^{13}C-SOC. Green colour represents the topsoil (0–10 cm) and the orange colour represents the subsoil (10–30 cm).

Figure S2. PCA ordination showing the relationship between plant diversity and soil depth in the topsoil (0–10 cm) and subsoil (10–30 cm), for (a) microbial PLFA composition and (b) bacterial and fungal markers. The microbial composition is shown as a mean value for each diversity treatment and soil depth with standard error bars.

Figure S3. Effects of plant diversity on the PC1 axis and plant diversity (log). Green colour represents the topsoil (0–10 cm) and the orange colour represents the subsoil (10–30 cm).

Figure S4. The effect of plant diversity on the PLFA biomass of (a) bacteria, (b) fungi and (c) arbuscular mycorrhiza fungi (AMF). Green colour represents the topsoil (0–10 cm) and the orange colour represents the subsoil (10–30 cm).

Figure S5. Effects of plant diversity on (a) bacterial turnover and (b) fungal turnover based on the PLFA biomass. Green colour represents the topsoil (0–10 cm) and the orange colour represents the subsoil (10–30 cm).

Figure S6. The effect of plant diversity on (a) bacterial growth resistance to drought and (b) fungal growth resistance to drought. The IC$_{50}$ value is estimated as the soil moisture (% WHC) when the bacterial or fungal growth were reduced by 50%. Green colour represents the topsoil (0–10 cm) and the orange colour represents the subsoil (10–30 cm). Significant plant diversity effects are indicated by solid lines, while non-significant effects are given with dashed lines.

Figure S7. Effects of plant diversity on the microbial carbon use efficiency (CUE) during the standardised drought for (a) CUE at 20% WHC and (b) CUE at 25% WHC. Green colour represents the topsoil (0–10 cm) and the orange colour represents the subsoil (10–30 cm). The CUE at the two different soil moisture levels was estimated by using the curvefit of the growth and respiration rates.

Table S1. ANOVA table showing the numerator and denominator degrees of freedom (DF), the *F* values and *p* values for the different linear mixed effects models (type I sum of squares).

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