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Both diversity and functional composition affect productivity and water use efficiency in experimental temperate grasslands

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Abstract

1. Many experiments have shown that biodiversity promotes ecosystem functioning and stability and that this relationship varies with resource availability. However, we still have a poor understanding of the underlying physiological and ecological mechanisms driving diversity effects and how they may interact with soil nutrient availability.

2. We collected data in a grassland experiment factorially manipulating fertilization, species richness (SR), functional composition (slow-growing vs. fast-growing species) and functional diversity in resource economic traits. We measured above-ground productivity (AP), nitrogen (N) uptake, photosynthesis and water use efficiency by combining a ^{15}N labelling approach with productivity, gas exchange and stable isotope measurements in 3 years differing in rainfall.

3. We found that sown SR increased AP, N uptake and photosynthesis, suggesting that SR is the most important driver of ecosystem productivity and nutrient cycling. Similarly, photosynthesis was affected by functional composition but not by functional diversity. Water use efficiency was reduced by sown SR for communities dominated by slow-growing species but not for communities dominated by fast-growing species. Fertilization increased productivity, N uptake and water use efficiency. The positive effects of high SR on ecosystem functions were independent of fertility levels.

4. *Synthesis.* Our results provide evidence that high species richness in temperate grasslands could enhance productivity and reduce the negative impacts of drought events. Multiple factors and community characteristics are important in

driving enhanced ecosystem functioning in biodiverse grasslands and seem to affect functioning and stability through different mechanisms.

KEYWORDS

^{13}C, ^{15}N, biodiversity–ecosystem functioning, complementarity, nitrogen uptake, photosynthesis, productivity, soil biogeochemistry

1 | INTRODUCTION

Many experimental studies have shown that biodiversity increases the functioning and stability of ecosystems (Cardinale et al., 2012; Hector et al., 1999; Tilman et al., 1996, 2006; Wang et al., 2019), and an increasing number of studies have shown that these results can be transferred to real-world ecosystems (Duffy et al., 2017; Jochum et al., 2020) Early studies focussed on species richness (SR) as the key dimension of biodiversity affecting functioning and stability, but more recent research has shown that other community properties, such as functional diversity or composition, are key drivers of functioning as well (e.g. Le Bagousse-Pinguet et al., 2019, Craven et al., 2018). Linking functional traits to ecosystem functioning and stability may allow a more mechanistic understanding of biodiversity effects (Cadotte, 2017).

Although many non-exclusive mechanisms can underlie the positive effects driving enhanced functioning in diverse communities (Barry et al., 2019), one of the most long-standing hypotheses is that biodiverse communities are complementary in their resource use (Tilman et al., 1996). Temporal, spatial and resource-specific complementarity between species could increase carbon, water and nutrient uptake of species in the community and lead to higher ecosystem-level productivity (Barry et al., 2019; Bessler et al., 2012; Loreau & Hector, 2001). Some indirect evidence of this process can be observed from studies showing that soil nitrogen (N) levels are lower in more diverse communities, suggesting that more efficient and complete nutrient uptake drives higher productivity (Fornara & Tilman, 2009). N is an essential, and often limiting nutrient, in agroecosystems, which directly affects plant N uptake, photosynthesis rates and eventually biomass production. However, direct evidence that resource use complementarity underlies the beneficial impact of diversity on productivity is sparse (e.g. Bachmann et al., 2015; Kleinebecker et al., 2014; Oram et al., 2018). Isotopic labelling studies, assessing ^{15}N uptake by plant roots, have suggested that N exploitation strategies differ between plants with contrasting functional traits (Kahmen et al., 2006). These findings suggest that functional diversity could be more critical in driving a positive biodiversity–productivity relationship and below-ground N resource partitioning than SR per se (e.g. Griffin et al., 2009, but see Jesch et al., 2018). However, whether diverse N exploitation strategies in species-rich communities leads to higher N uptake, resulting in higher photosynthesis, and consequently, biomass production, remains unclear.

The presence of species with particular functional traits (i.e. functional composition) should also strongly affect functioning and resource uptake levels in terrestrial ecosystems. The leaf economics spectrum is one of the key axes of plant functional variation: it distinguishes slow-growing, conservative species (with low SLA and foliar N content) from fast-growing acquisitive species (with high SLA and foliar N content, Díaz et al., 2016; Wright et al., 2004). The slow-growing species are usually more competitive in resource-poor environments and are more drought tolerant (Craven et al., 2018), which might mean that they are more efficient in their resource uptake. This would mean that communities composed mainly of slow-growing species (i.e. those with low average SLA and/or foliar N content), from low-resource environments, might also differ more in their strategies to exploit resources, such as N and water (Tilman, 1985). At the other end of the spectrum, fast-growing species are more competitive in nutrient-rich environments where competition for light is the predominant factor shaping communities (Hautier et al., 2009). Fast-growing species are likely to invest in strategies to maximize light capture rather than nutrient uptake, and below-ground complementarity might therefore be reduced in grasslands primarily composed of fast-growing light-competitive species. Furthermore, species composition and richness could alter ecosystem functions through other trait-based processes that are not associated with leaf economic traits, such as rooting depth, hydraulics or phenology. Yet, we know very little about how SR, functional diversity and functional composition interact to alter plant community resource use and biomass production, largely because few experiments have manipulated these factors separately.

Differences in resource use strategies between species may also allow diverse communities to better resist extreme climatic events, such as drought (Oliver et al., 2015). However, the evidence for this is somewhat mixed. Recent studies have found that diversity increases drought resistance and exposure (Cole et al., 2019; Isbell et al., 2015), but adverse effects have also been found (Pfisterer & Schmid, 2002). Functional composition and diversity have been shown to be important drivers of ecosystem stability in terms of persistence (i.e. the ability to sustain stable function across time) but have rarely been linked to drought exposure (Craven et al., 2018). Drought exposure is related to water use efficiency as plants need to optimize the trade-off between taking up carbon through photosynthesis and water loss through transpiration during periods of limited soil moisture. When exposed to drought stress,

plants therefore tend to reduce stomatal conductance to a larger extent than CO_2 assimilation, leading to a concomitant increase in water use efficiency (Ehleringer, 1993; Farquhar et al., 1989). Thus, plants and ecosystems with higher water use efficiency, as indicated by less negative tissue carbon isotope composition ($\delta^{13}C$) under water limitation, are thought to be less limited in their functioning by water availability and can therefore be considered to be less drought exposed (e.g. Gessler et al., 2007; Grossiord et al., 2014). The underlying mechanisms driving the effects of diversity on water use efficiency could include more extensive partitioning (complementarity) of soil water sources through differential rooting depths or the greater likelihood that drought-tolerant species are present in more diverse systems (Mariotte et al., 2013; Pacala & Tilman, 2002). As discussed above, slow-growing species might differ more in their water use strategies than fast-growing species. Slow-growing species might therefore be more resistant to drought overall, and a high diversity of slow species might be particularly resistant to drought.

If resource use complementarity underlies the positive effects of biodiversity on productivity and stability, we might expect that resource addition would strongly affect biodiversity–ecosystem functioning relationships. Chronic N input, driven by rising atmospheric deposition and increased fertilizer use, has substantial impacts on terrestrial ecosystems. This includes direct effects on soil nutrient content and plant physiology (Manning et al., 2006) and indirect effects such as shifting communities towards dominance by fast-growing acquisitive species (Clark et al., 2007; Hautier et al., 2014) and causing biodiversity loss (Brunsting & Heil, 1985; Carroll et al., 1999; Hautier et al., 2009; Isbell et al., 2013). Furthermore, N enrichment is known to reduce plant investments in below-ground compartments (e.g. Heyburn et al., 2017), thereby potentially decreasing root spatial partitioning. In the short-term, fertilization was found to strengthen or have no impact on the relationship between biodiversity and productivity in experimental grasslands (Craven et al., 2016; Weigelt et al., 2009; Weisser et al., 2017). In the longer term, biodiversity effects may be reduced as fertilization reduces N limitation and further promotes fast-growing acquisitive species that are more competitive for light (Hautier et al., 2009), both resulting in reduced complementarity for resources. However, the effects of N addition on the relationship between biodiversity and ecosystem functioning and the underlying physiological and biological drivers are still not well-understood.

To address these questions, we investigated the independent and interactive impacts of SR, functional composition and diversity (in leaf economic traits) and N fertilization on ecosystem functioning [community-level above-ground productivity (AP)] and water use efficiency. We explored the mechanisms behind treatment effects by looking at community-level N uptake, photosynthesis and water use efficiency. We used a unique grassland biodiversity experiment where SR, functional composition (a gradient from fast- to slow-growing species), functional diversity (in leaf economic traits) and N addition are factorially manipulated in the field, allowing their relative impacts to be assessed. We combined a ^{15}N labelling approach

with assessments of productivity, community-level photosynthesis and stable isotope measurements. Here, we tested the following hypotheses:

1. Complementarity in N exploitation, resulting in higher community-level N and carbon uptake, helps explain why AP is significantly higher in more diverse plots (i.e. higher SR and functional diversity) than in species-poor ones. Compared to fast-growing species assemblages, communities dominated by slow-growing species will have lower productivity, N uptake and photosynthesis.
2. A better partitioning of water resources, resulting in reduced soil moisture stress, should lower the water use efficiency of more diverse plots (i.e. higher SR and functional diversity), relative to less-diverse ones. Communities dominated by slow-growing species are expected to be less drought exposed due to complementary exploitation of water resources, which will result in a lower water use efficiency relative to communities dominated by fast-growing species.
3. Fertilization will dampen the positive diversity effects on productivity and water use efficiency by reducing N and water use complementarity, resulting in similar community-level N uptake, photosynthesis, water use efficiency and productivity in fertilized compared to non-fertilized, high diversity plots (i.e. high SR and functional diversity).

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in a grassland experiment (PaNDiv experiment), which aims to investigate the independent and interactive impacts of N fertilization, SR, functional diversity and functional composition on ecosystem functioning (see Pichon et al., 2020). The experiment is located 10 km northwest of Bern in Münchenbuchsee (47°03′N, 7°46′E, 564 m a.s.l.). The mean annual temperature is approx. 9.2°C and mean annual precipitation is about 1,052 mm (30 years average by the Federal Office of Meteorology and Climatology MeteoSwiss). The soil is characterized as brown soil with a thickness of about 70 to 100 cm (Geoportal of the Canton Bern, https://www.geo.apps.be.ch/de/). The site was arable land until about 15 years ago when it was converted to extensively managed grassland. After vegetation removal and plowing, the PaNDiv experiment was established in 2015. The species growing at the site were all sown in autumn 2015 on bare soil. The sown species consist of a pool of 20 non-leguminous species found in extensively and intensively managed Central European grasslands and are composed of 10 fast-growing and 10 slow-growing species, with the functional groups defined according to their leaf economic traits, SLA and leaf N content (Table S1). Both fast-growing and slow-growing species consist of six forbs and four grasses. The design specifically excludes legume species as their high leaf nutrient

values would put them in the fast-growing pool, and this would cause an additional difference between fast and slow species (N fixation or not). Further, legumes would be expected to decline with N fertilization, in contrast to the other fast-growing species which are predicted to increase. The experiment was weeded three times per year (April, July and September) to maintain the species compositions (species abundances could change over time but compositions are relatively fixed) and was mown twice per year, around the 15 June and 15 August.

The experiment consists of 336 plots (2 m × 2 m), arranged randomly in four blocks; however, for this study, only 168 plots were used (the experiment also contains a fungicide treatment, but only the unsprayed plots were used here). The experiment manipulates SR, functional composition and N fertilization in a full factorial design (each treatment combination is repeated at least four times). N fertilization was applied twice per year since 2015 by adding of 50 kg N/ha (i.e. a total of 100 kg N ha^{-1} year^{-1}), corresponding to intermediately intensive management (Blüthgen et al., 2012). The control treatment has 3.6 ± 0.4 g N/kg soil, which is slightly higher than in similar experiments (Scherer-Lorenzen et al., 2003; Weisser et al., 2017). To manipulate SR, plots were planted with 1, 4, 8 or 20 species.

The functional composition was manipulated by assembling experimental communities, using only fast-growing, only slow-growing or a mix of fast- and slow-growing species. The particular species composition of each plot was random, as species were randomly selected from the particular species (slow, fast or all species), meaning that effects of SR and functional composition and diversity are independent of species composition. The functional composition manipulation created a large gradient in community-weighted mean SLA (CWM$_{SLA}$, weighted by relative cover of sown species determined few days prior to mowing) and in functional diversity (as plots with both fast- and slow-growing species had higher functional diversity). We used CWM$_{SLA}$ as the measure of functional composition as CWMs are commonly used to represent the overall community value of a trait (see Garnier et al., 2004; Violle et al., 2007). High values of CWM$_{SLA}$ indicate a community dominated by fast-growing species.

To calculate functional diversity, we used the mean species pairwise distance (MSPD), which was calculated from unfertilized monoculture SLA and above-ground tissue N content weighted by species abundance. In detail, MSPD was calculated using the 'melodic' function provided by de Bello et al. (2016), and thus, represents the weighted dissimilarity in trait values of a given community. A high MSPD reflects communities in which individuals differ substantially in the resource economic traits, that is those with a high functional diversity. The factorial design crossing SR and functional composition with CWM$_{SLA}$ and MSPD is shown in Figure S1 and in Figure S2 respectively.

2.2 | Above-ground productivity

Sampling of the above-ground biomass took place in the second week of June 2019 (i.e. 4 years after the experiment was established).

In all 168 plots, biomass was sampled in two 20 cm × 50 cm rectangles, and plants were cut 5 cm above the ground. Edge effects were avoided by placing the sampling rectangles 50 cm from the edge of the plot. The samples were stored in vented plastic bags and dried for 48 hr at 65°C before measuring dry mass (using the balance PM4800, Mettler-Toledo). Above-ground productivity (g/m^2) was calculated based on the average dry biomass across the two replicates. Percentage cover of all target (sown species) plus the total cover of weeds (non-target species) was estimated visually in the central 1 m^2 of each plot in late May. Different people estimated the cover, but a single person always assessed each block, meaning we could statistically correct for recorder differences by including block in the analysis. All cover estimates were converted to relative values for the analyses. To correct the biomass for the weed cover, the relative percentage of weeds per plot was removed from the total biomass weight in each plot. However, weed percentages were low (around 5% on average), so this correction did not substantially change the biomass. Overyielding (D$_{mean}$, unitless) and transgressive overyielding (D$_{max}$, unitless) were calculated from AP. D$_{mean}$ is the ratio between observed AP and predicted AP from the weighted average of the monoculture yields of the component species and D$_{max}$ is the ratio between observed AP and predicted AP from the most productive component species.

2.3 | Plant nitrogen uptake

2.3.1 | Application of the ^{15}N-label

Two weeks before the above-ground biomass sampling, a ^{15}N-ammonium-^{15}N-nitrate solution (^{15}NH$_4$^{15}NO$_3$; 98 atom% ^{15}N purity; Sigma-Aldrich) was applied as a label in all 168 plots to track the total uptake of inorganic nitrogen (N uptake). The amount of the ^{15}NH$_4$^{15}NO$_3$ solution applied to each plot was chosen to equal 5% of the average plant-available N in the topsoil layer (0–10 cm) in unfertilized plots, to avoid substantial dilution in the soil and plant material and to avoid fertilization effects (Fotelli et al., 2004). A total of 38.6 µg of ^{15}NH$_4$^{15}NO$_3$ was applied to the weeded part of each plot (3 m^2, a 1-m^2 strip is left unweeded in each plot) dissolved in 6 L of tap water, thereby simulating a 2 mm precipitation event. No rinsing was applied to the plots after label application, so our estimation of total N uptake could include soil and foliar N uptake, particularly as the first rain event occurred 2 days after label application.

2.3.2 | Soil sampling

In the week before the ^{15}N label application, we sampled soil to characterize the natural level of δ^{15}N, inorganic N concentrations (nitrate and ammonium), total carbon (TC) and total N (TN). In all 168 plots, three soil cores were taken at random locations with a 4-cm diameter soil auger (depth 0–15 cm). An additional subset of 36 plots was sampled

between 15 and 30 cm using the same methodology and locations to quantify the natural level of $\delta^{15}N$ deeper in the soil. All soil cores from a given depth and plot were pooled together and kept inside cooling boxes before being stored at 5°C in the laboratory. All 168 soil samples of 0–15 cm depth were split into two subsamples for further analyses of soil inorganic N. A second soil sampling took place 2 weeks after the ^{15}N label application, where only the subset of 36 plots was sampled at two depths (0–15 cm and 15–30 cm) to determine how much label remained in the soil. Mean soil pH was 5.7 in 2019.

2.3.3 | Soil inorganic N

The soil subsamples collected during the first campaign were sieved moist through a 4-mm sieve, and the plant debris was removed. A 5 g aliquot of each sample was then used to determine the soil's gravimetric water content by weighing the moist mass of this aliquot, drying it at 105°C for 48 hr, and then weighing it again. Extractable inorganic N concentrations (nitrate, NO_3^- and ammonium, NH_4^+) of the moist soil were determined by adding 40 ml of 1 M KCl to 7.5 g dry soil equivalent. The samples were agitated for 1.5 hr on an overhead shaker and filtered. The ammonium and nitrate concentrations were determined by UV/VIS spectroscopy. For the determination of ammonium concentration, subsamples with a dilution factor of 1:4 were prepared. These subsamples were then injected into the UV/VIS 2S spectrophotometer using a FIAS 400 (Perkin Elmer, Waltham, Massachusetts, USA), and ammonium concentrations were measured. For the determination of the nitrate concentration, subsamples with a dilution factor of 1:3 (and in few cases 1:6) were prepared. The nitrate concentrations were determined using a Cary 60 UV/VIS (Agilent Technologies, Santa Clara, California, USA). All inorganic N measurements were calculated using at least two replicates. If the difference between replicates was higher than 10%, another two replicates were measured. NH_4^+ and NO_3^- concentrations were transformed into µg/g of dry soil using the gravimetric soil water content values.

2.3.4 | Isotope ratios and label uptake

The dry above-ground biomass samples used to estimate AP were carefully rinsed using tap water to avoid remaining label on the leaf surface. They were dried for 48 hr at 65°C. The samples were then ground to a fine powder using a PULVERISETTE 16 (Frisch, Idar-Oberstein, Germany) and an MM400 grinder (Retsch, Haan, Germany). The soil samples were dried at 65°C for 48 hr, ground to a fine powder using a porcelain mortar, and sieved at 250 µm. Bulk N isotope concentration ($\delta^{15}N$, ‰), TC and TN content (%) of the dried above-ground biomass and the dried soil were determined from 1 ± 0.1 mg of dried plant material and 5 ± 0.2 mg of soil material packed in tin capsules. The samples were analysed using an elemental analyser coupled with an isotope-ratio mass spectrometer (EA-IRMS; Thermo EA 1100 Delta^{plus} XL; 0.3 ‰ precision for

$\delta^{15}N$). Bulk TN and TC were measured from 25 ± 0.2 mg of soil using an elemental analyser for the 132 samples not investigated for $\delta^{15}N$ (Thermo Quest NC 2500). The uptake of ^{15}N label (N uptake, mg/m^2) was estimated using Equations 1 and 2 following Ruehr et al. (2009):

$$\text{atom}\% = \frac{100 * R_{standard} \times \left(\frac{\delta^{15}N}{1,000} + 1\right)}{1 + R_{standard} \times \left(\frac{\delta^{15}N}{1,000} + 1\right)}, \tag{1}$$

$$N_{uptake} = \frac{\text{atom}\%_{sample} - \text{atom}\%_{background}}{100} \times M \times \frac{N\%}{100}, \tag{2}$$

with $R_{standard}$ being the standard value for the isotope ratio of N_2 in air, M is the above-ground biomass per square meter and $N\%$ is the percentage N in above-ground biomass. The natural ^{15}N background concentrations of above-ground biomass (atom%$_{background}$) were determined for each plot using the above-ground biomass from June 2017 (dried plant material was sampled in all plots in 2017 using the same protocol). This procedure was chosen as it would not have been possible to immediately sample the biomass before applying the label, which would have caused too much disturbance to the experiment. There were only small changes in functional group cover within plots between 2017 and 2019 (Figure S3a–c) and these differences are much smaller than the difference in functional composition between plots. Therefore, using values from a previous year should not affect the results, as the natural variability in ^{15}N contents over time is small relative to the changes caused by applying the label, and changes in species composition through time will be small relative to differences in composition between plots.

2.4 | Maximum CO$_2$ assimilation rate

The maximum CO$_2$ assimilation rate (A_{max}, µmol m^{-2} s^{-1}) was determined on all species (one individual per species) inside a plot during sunny days over 2 weeks in June 2019 using three LI-6400XT Portable Photosynthesis System (LI-COR Inc.). Measurements were conducted on a subsample of 105 plots, which were selected to represent the two fertilization treatments (53 non-fertilized and 52 fertilized plots), all SR levels including all monocultures and combinations of 4-, 8- and 20-species plots (37, 30, 30 and 8 plots in the 1, 4, 8 and 20-species plots respectively), and a large gradient of MSPD (from 0 to 0.51) and CWM$_{SLA}$ (from 8 to 36). Three monoculture plots were excluded because they had very low plant cover, which did not permit gas exchange measurements. Measurements were conducted with the following settings with the 2×3 LED chamber: 400 ppm of reference CO$_2$ concentration, 1,500 µmol m^{-2} s^{-1} light-saturating photosynthetic photon flux density, block temperature at 25°C to match ambient air temperature and relative humidity at 50% to match ambient air humidity. Leaf temperature was measured using the energy balance. Measurements were recorded after steady-state gas exchange rates had been maintained for at

least 2 min. The projected leaf area of the measured foliage was determined using a scanner (Perfection V800 Photo, EPSON, Suwa, Japan), and was used to correct the maximum CO_2 assimilation rate of each species inside a plot. Plot-level maximum CO_2 assimilation rate (P_{Amax}) was calculated by averaging individual species assimilation rates and considering the relative proportion in total cover for each species.

2.5 | Plant water use efficiency

We measured the carbon isotope composition ($\delta^{13}C$, ‰) of the bulked above-ground biomass from three subsequent years to estimate each plot's water use efficiency. To avoid hydraulic damage during drought, plants respond by closing their stomata and reducing photosynthesis. The carbon isotopic composition in plant tissues ($\delta^{13}C$) provides an integrated record of the ratio of intercellular to atmospheric CO_2 concentrations during the period when the carbon was fixed. $\delta^{13}C$ thus reflects the balance between net CO_2 assimilation and stomatal conductance (Ehleringer & Cooper, 1988; O'Leary, 1995). $\delta^{13}C$ is therefore commonly used as an indicator of water use efficiency (Keitel et al., 2003). If diverse plant communities can keep stomata open for longer and are thus less efficient in water use, for example, due to higher water uptake complementarity, $\delta^{13}C$ values should decrease significantly with increasing plant diversity.

The $\delta^{13}C$ of each plot was determined from 1 ± 0.1 mg of homogenized dried plant material (Mettler MT5) packed in tin capsules. As we used the bulked biomass, the changes in water use efficiency include both effects related to shifts in species composition and cover (Figure S3), and within-species changes in water use efficiency in response to the treatments. Such a bulking approach allows us to estimate overall community-level water use efficiency, without having to consider individual species contribution (in leaf area) as was done in previous work (e.g. Grossiord et al., 2013). The samples were analysed using an EA-IRMS (Thermo EA 1100 Delta^{plus} XL; 0.1‰ precision for $\delta^{13}C$). Measurements were conducted on plant material collected once per year over 3 years (2017–2019), all of which differed in precipitation levels. Plant material was collected in June 2017 (water balance over 3 months before sampling was equal to 0 mm), August 2018 (water balance over 3 months before sampling was equal to −98 mm) and June 2019 (water balance over 3 months before sampling was equal to 92 mm) using the same procedure as described in Section 2.3. The long-term water balance average (1901–1990) in spring and summer is equal to 110 mm and 159 mm respectively (Brändli, 1993). Plant material was collected during a different season in 2018 compared to 2017 and 2019 to include a dry period and allow comparison of three distinct soil moisture conditions. Although species composition does vary between June and August, with different species dominating the communities in August (data not shown), these changes are small relative to compositional differences between plots. The water balance

was calculated as the difference between precipitation and potential evapotranspiration measured at the nearby meteo station Zollikofen (Precipitation bulletins, Federal Office of Meteorology and Climatology MeteoSwiss).

2.6 | Data analysis

All statistical analyses were performed using the software R (4.0.2, R Core Team, 2020). Responses of all variables (i.e. AP, P_{Amax}, N uptake, $\delta^{13}C$, soil NH_4^+, soil NO_3^-, soil C/N, soil $\delta^{15}N$) were analysed using linear mixed effect models. Some dependent variables were log-transformed (soil $\delta^{15}N$, NH_4^+ and NO_3^-) or square root-transformed (AP, P_{Amax} and N uptake) to ensure normality and homoscedasticity in the residuals. Fixed effects were the experimental treatments: fertilization (F), SR (1, 4, 8, 20 species), functional composition (community-weighted mean SLA, CWM_{SLA}) and functional diversity (mean pairwise distance, MSPD) as well as all possible interactions between them (except for the interaction between MSPD and CWM_{SLA}, which we excluded as these two variables are inevitably correlated: maximum MSPD is only possible at intermediate CWM_{SLA}). All models use log-transformed SR to take into account the nonlinear relationship of SR with dependent variables. For soil $\delta^{15}N$, the sampling depth (0–15 and 15–30 cm) was also included as a fixed effect. For plant $\delta^{13}C$, the water balance of the sampling year and the bare ground cover of each plot were included. Block and the specific-species combination (ID) were used as random effects for all models, and plot was used as a random effect for soil $\delta^{15}N$ and plant $\delta^{13}C$. The best model was selected stepwise, removing the variables with the lowest explanatory power, and comparing models using likelihood ratio tests. We derived *p*-values for all terms in the final model by dropping them individually from the model and comparing models using likelihood ratio tests. The packages used for the data analysis were *onewaytest* for analysis of heteroscedasticity and *lme4* for model evaluation (Bates et al., 2015).

3 | RESULTS

3.1 | Above-ground productivity

Fertilized plots (F) had one third higher productivity than unfertilized ones (Table 1, $p < 0.001$). Higher sown SR ($p = 0.003$) increased AP (Figure 1a), while functional diversity (i.e. mean pairwise distance, MSPD) and functional composition (i.e. community-weighted mean SLA, CWM_{SLA}) had no impact (Figure 1b,c). However, the most productive plots were the unfertilized monoculture of *Festuca rubra* and the fertilized four species mixture of *Dactylis glomerata*, *Galium album*, *Heracleum sphondylium* and *Rumex acetosa*. We found overyielding across all SR and fertilization levels, whereas transgressive overyielding decreased with SR and was higher for fertilized plots (Table S2, Figure S4). No

TABLE 1 Summary of the linear mixed-effects models of above-ground productivity (AP), nitrogen uptake (N uptake), plot-level maximum CO_2 assimilation (P_{Amax}), leaf carbon isotopic composition ($\delta^{13}C$) and soil ammonium (NH_4^+). No significant effects were found for soil nitrate concentration (NO_3^-) and soil C/N, thus the models are not presented in the table. F stands for fertilization, SR stands for species richness, CWM_{SLA} stands for community-weighted mean specific leaf area, MSPD stands for mean species pairwise distance and BG stands for bare ground cover. Given are mean sums of squares (MS), degrees of freedom (df), Wald χ^2 and p-values. The dependent variables for all models (except $\delta^{13}C$) have been transformed

	Random effect ± SD	Fixed effect ± SE		MS	df	Wald χ^2	p-value
AP[a]	(1|Block) ± 1.03	*Intercept*	15.23 ± 1.06				
	(1|Identity) ± 2.75	F	2.67 ± 0.69↑	290.00	1	14.26	<0.001
		log(SR)	1.97 ± 0.55↑	247.68	1	12.30	0.003
N uptake[a]	(1|Block) ± 0.01	Intercept	1.23 ± 0.08				
	(1|Identity) ± 0.02	F	0.24 ± 0.05↑	2.40	1	18.64	<0.001
		log(SR)	0.16 ± 0.04↑	2.19	1	17.16	0.001
NH_4^{+a}	(1|Block) ± 0.04	*Intercept*	1.82 ± 0.10				
	(1|Identity) ± 0.00	F	0.15 ± 0.04↑	1.12	1	14.20	<0.001
		log(SR)	0.10 ± 0.03↑	0.26	1	9.59	0.002
		MSPD	−0.56 ± 0.22↓	0.43	1	8.03	0.010
		CWM_{SLA}	−0.01 ± 0.00↓	0.41	1	6.60	0.005
P_{Amax}[a]	(1|Block) ± 0.03	*Intercept*	4.94 ± 0.33				
	(1|Identity) ± 0.00	log(SR)	0.41 ± 0.07↑	19.16	1	23.10	<0.001
		CWM_{SLA}	−0.08 ± 0.01↓	16.42	1	27.67	<0.001
$\delta^{13}C$	(1|Block) ± 0.18	*Intercept*	−29.35 ± 0.29				
	(1|Identity) ± 0.25	F	0.18 ± 0.06↑	0.68	1	9.53	0.002
	(1|Plot) ± 0.11	log(SR)	−0.53 ± 0.19↓	7.70	1	7.53	
		CWM_{SLA}	0.00 ± 0.01↑	3.10	1	0.06	
		BG	0.01 ± 0.00↑	11.67	1	30.83	<0.001
		log(SR):CWM_{SLA}	0.02 ± 0.01↑	1.73	1	4.62	0.032

[a]For AP, N uptake and P_{Amax}, square root transformation has been used, whereas NH_4^+ was transformed using the natural logarithm.

significant interactions between fertilization and SR, MSPD and CWM_{SLA} were found, suggesting that fertilization did not influence the effects of diversity on productivity.

3.2 | Nitrogen uptake

The amount of label incorporated in above-ground biomass (N uptake) varied between 0.60 mg/m^2 and 7.74 mg/m^2. Fertilized plots took up significantly more inorganic N than unfertilized ones (Table 1, $p < 0.001$) and higher SR led to an increase in inorganic N uptake ($p = 0.001$, Figure 2a). However, the interaction between fertilization and richness was not significant, suggesting that fertilization did not influence diversity effects on N uptake. No effects of MSPD and CWM_{SLA} were observed (Figure 2b,c), meaning that functional composition and diversity did not affect N uptake.

The application of the N label led to a positive $\Delta^{15}N$ (i.e. an increase in $\delta^{15}N$) in the entire investigated soil profile (0–15 and 15–30 cm, $p < 0.001$). This increase was more pronounced in the uppermost 15 cm (with an average $\Delta^{15}N$ of 8.0 ‰) in comparison to the deeper soil layer ($\Delta^{15}N$ of 4.8 ‰; $p < 0.001$, Figure S5). Soil $\Delta^{15}N$

decreased with SR ($p < 0.043$), but no effect of the treatments F, CWM_{SLA} and MSPD, or any interactions were found.

3.3 | Plot-level CO_2 assimilation rate

Plot-level maximum CO_2 assimilation rate (P_{Amax}) ranged from 1.5 to 38.5 µmol m^{-2} s^{-1}. P_{Amax} significantly increased with SR ($p < 0.001$) and decreased with CWM_{SLA} ($p < 0.001$, Figure 3a,c). No effects of fertilization, MSPD or any interactions between factors were found for P_{Amax} (Figure 3b; Table 1). We tested the relationship between P_{Amax} and AP considering CWM_{SLA} and fertilization levels but did not find any trends (Figure S6).

3.4 | Plant water use efficiency

The interaction between SR and CWM_{SLA} ($p = 0.032$) significantly impacted $\delta^{13}C$: increasing SR decreased plant $\delta^{13}C$ (i.e. species-rich plots are less water-efficient) at low CWM_{SLA}, while it increased plant $\delta^{13}C$ at high CWM_{SLA} (i.e. plots dominated by fast-growing species are more water use efficient, Figure 4a). A significant effect
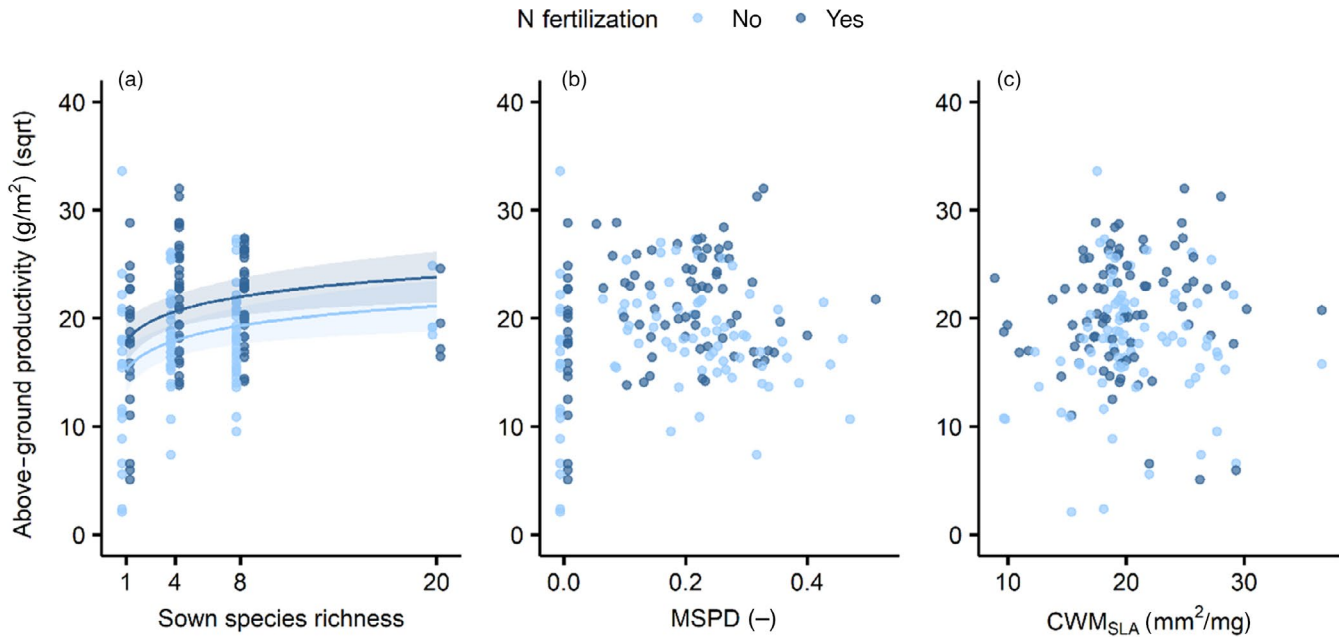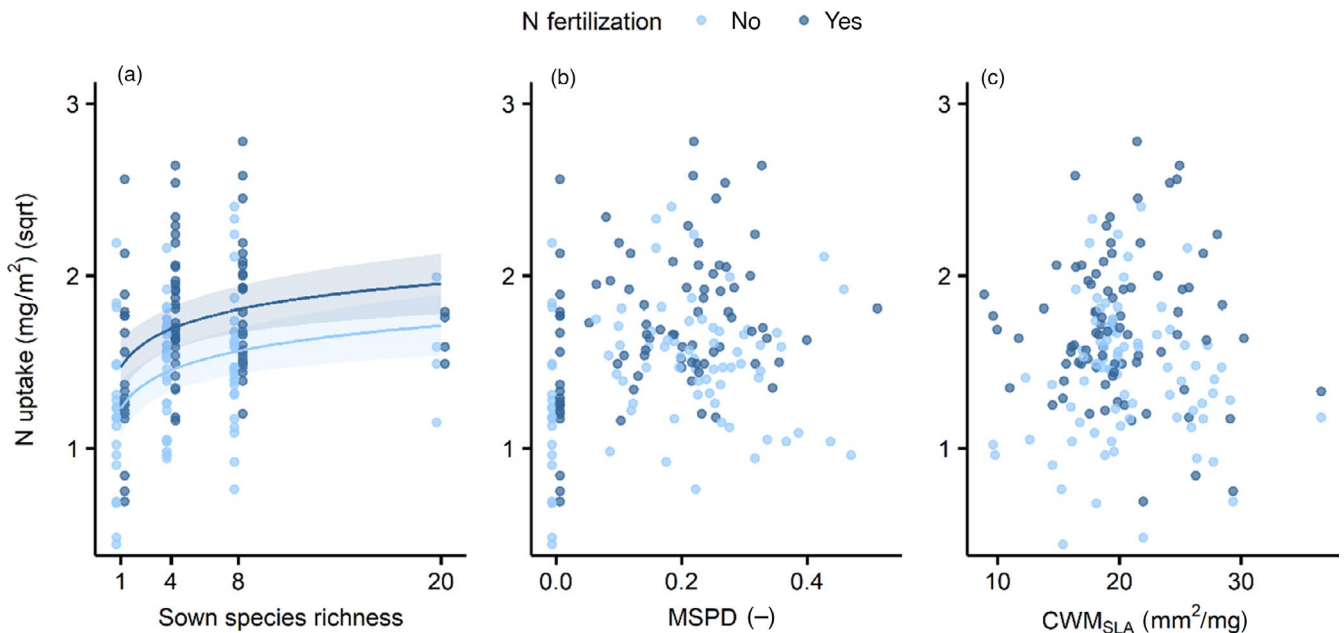
FIGURE 1 Effects of sown species richness (a), functional diversity (b, MSPD) and functional composition (c, CWM$_{SLA}$) on above-ground productivity (AP). The predicted relationships from the final model are represented as solid lines with corresponding 0.95 confidence intervals around the prediction. The dependent variable (AP) in the model represents square root-transformed values to respect the normal distribution and homoscedasticity. A significant effect was found for sown species richness ($p = 0.003$), whereas no significant effect for MSPD and CWM$_{SLA}$ was found. Panels without regression line indicate that the fixed effect was eliminated from the model before the final model was obtained

FIGURE 2 Effects of sown species richness (a), functional diversity (b, MSPD) and functional composition (c, CWM$_{SLA}$) on nitrogen uptake (N uptake). The predicted relationships from the final model are represented as solid lines with corresponding 0.95 confidence intervals around the prediction. The dependent variable (N uptake) in the model represents square root-transformed values to respect the normal distribution and homoscedasticity A significant effect was found for sown species richness ($p = 0.001$), whereas no significant effect for MSPD and CWM$_{SLA}$ was found. Panels without regression line indicate that the fixed effect was eliminated from the model before the final model was obtained

of fertilization was found for $\delta^{13}C$ ($p = 0.002$, Table 1), implying that fertilization increased water use efficiency. No effects of water balance, MSPD or any interactions between other factors were found for $\delta^{13}C$ (Figure 4b). Plant $\delta^{13}C$ was unaffected by AP (Figure S7).

Plant $\delta^{13}C$ was significantly influenced by bare ground area, with more positive $\delta^{13}C$ values for plots with lower plant cover ($p < 0.001$, Figure 4c), indicating increased plant water use efficiency with decreasing plant coverage (Table 1).
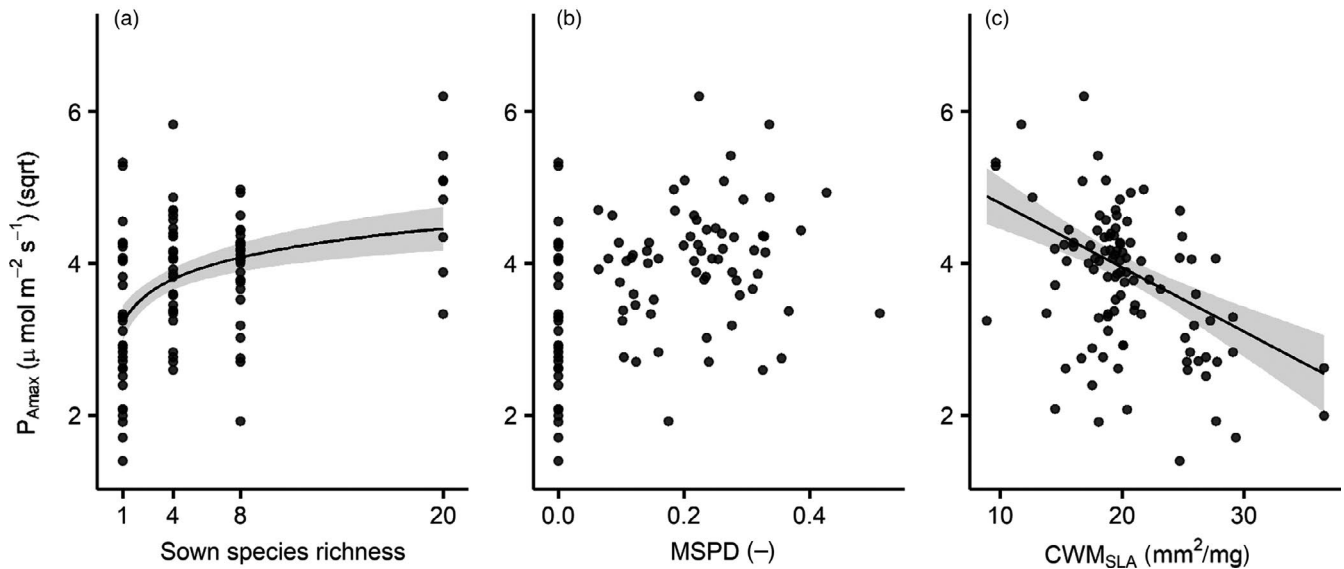
FIGURE 3　Effects of sown species richness (a), functional diversity (b, MSPD) and functional composition (c, CWM_{SLA}) on plot-level maximum CO_2 assimilation rate (P_{Amax}). The predicted relationships from the final model are represented as solid black lines with corresponding 0.95 confidence intervals around the prediction. The dependent variable (P_{Amax}) in the model represents square root-transformed values to respect the normal distribution and homoscedasticity. A significant effect was found for sown species richness ($p < 0.001$) and CWM_{SLA} ($p < 0.001$), whereas no significant effect of MSPD was found. Panels without regression line indicate that the fixed effect was eliminated from the model before the final model was obtained

FIGURE 4　Effects of the interaction of sown species richness and functional composition (CWM_{SLA}, a), functional diversity (b, MSPD) and bare ground cover (c) on carbon isotopic composition ($\delta^{13}C$). The predicted relationships from the final model are represented as solid lines with corresponding 0.95 confidence intervals around the prediction. Panel a shows a colour gradient covering all measured CWM_{SLA} levels and a prediction for high CWM_{SLA} (blue) and low CWM_{SLA} (black) on $\delta^{13}C$ with increasing sown species rich ($p = 0.032$). We observed a significant effect of bare ground on $\delta^{13}C$ ($p < 0.001$), whereas no significant effect for MSPD and was found. Panels without regression line indicate that the fixed effect was eliminated from the model before the final model was obtained
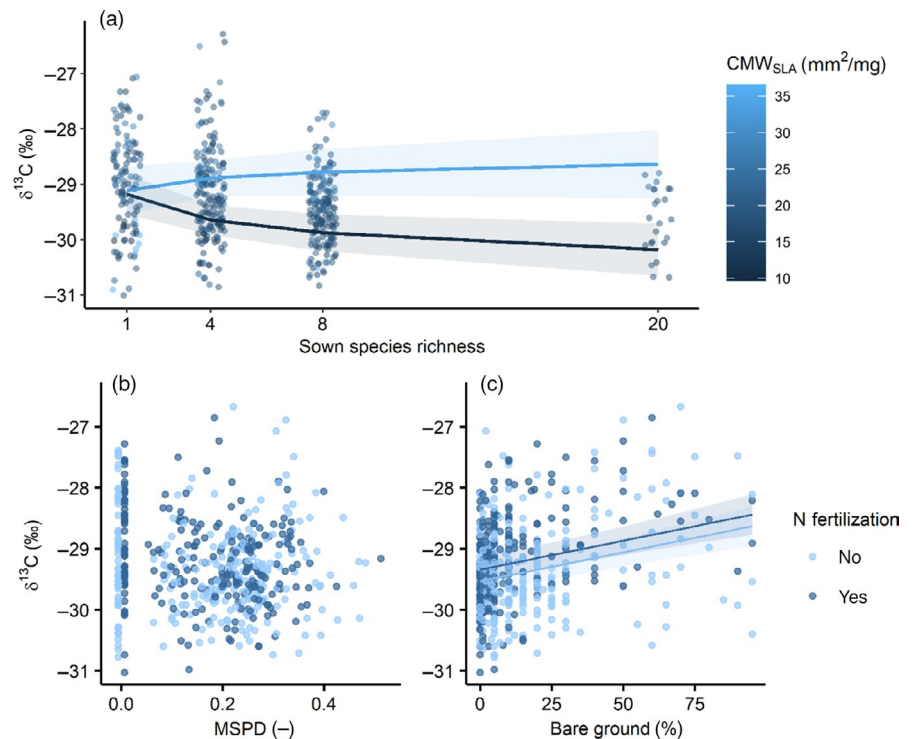
3.5 | Soil biogeochemistry

The ammonium concentration in the uppermost soil layer (0–15 cm) ranged from 3.0 to 13.8 µg/g with a significantly higher ammonium concentration in fertilized plots compared to unfertilized ones ($p < 0.001$). Soil ammonium content significantly increased with SR and decreased with MSPD ($p = 0.002$ and $p = 0.010$) and was influenced by CWM_{SLA} ($p = 0.005$), where an increase in CWM_{SLA} decreased soil ammonium content (Figure S8a–c; Table 1). The nitrate concentrations were exceedingly heterogeneous between plots, varying between 23.3 µg/g and 215.0 µg/g, and did not differ between treatments (Figure S8d–f). Total C and N concentrations in the uppermost soil layer varied between 2.35% and 4.70% and between 0.25% and 0.43% respectively. The soil C/N ratios were low,

with most plots exhibiting C/N ratios below 10. Soil C/N ratios were not affected by any treatment (Figure S8g–i).

4 | DISCUSSION

4.1 | Impact of diversity, functional composition and fertilization on productivity, nitrogen uptake and photosynthesis

Understanding the underlying physiological and ecological mechanisms responsible for the positive biodiversity–productivity relationship is critical to gain mechanistic insight and predict what shapes this relationship across landscapes. In line with many previous studies (e.g. Hector et al., 1999, Loreau et al., 2001, and Tilman et al., 2001), our work revealed that higher SR is associated with increased AP (Figure 1). However, in contrast to others (e.g. Cadotte, 2017; Flynn et al., 2011; Mouillot et al., 2011), we did not find an effect of functional diversity (MSPD) on productivity. Most other studies relating functional diversity to ecosystem functioning characterize functional diversity based on a number of different traits, representing different functional strategies, for example leaf economics, size, root traits, etc. In our study, we focused on functional diversity (MSPD) considering only leaf economic traits (i.e. leaf N content and SLA), as these are explicitly manipulated in the PaNDiv experiment and are expected to link to resource uptake. The lack of effect of functional diversity may therefore suggest that diversity in other functional characteristics (e.g. root traits or traits associated with responses to specialist herbivores or pathogens) could contribute to the positive effect of SR on AP. We also found that plot-level photosynthesis, which is directly driving productivity, increased with SR but not with functional diversity (i.e. MSPD, Figure 3). Hence, the diversity of fast-slow leaf traits did not capture the underlying mechanisms contributing to enhanced carbon uptake, and thus productivity, in species-rich ecosystems. Underlying mechanisms could include many unmeasured traits linking to higher light, nutrient and water uptake and use in species-rich plant communities.

Higher SR also led to an increase in N uptake (Figure 2a) and soil ammonium concentrations (Figure S8a), perhaps suggesting that similar underlying factors must be driving carbon and N uptake rates. The increase in ammonium concentration with sown SR might be related to higher microbial biomass, and especially turnover, in species-rich grassland communities (Prommer et al., 2020). High microbial turnover might lead to increased ammonium concentrations due to increased microbial decomposition rates. While SR had an impact, the diversity in leaf economic traits did not affect N uptake (Figure 2b). These findings contradict previous work (von Felten et al., 2009; Kahmen et al., 2006; Miller et al., 2007), where co-occurring grassland species were shown to partition soil N pools. Complementarity effects that allow more complete use of available soil N could occur spatially (i.e. differences in rooting depths), temporally (i.e. temporal differences in N uptake; McKane et al., 2002) and/or be resource specific (i.e. partitioning of different N forms). Our results suggest

that resource economic traits may not capture these differences in resource uptake very well and other axes of functional trait variation may be important (e.g. Bergmann et al., 2020). Future work that includes specific physiological traits (i.e. plant rooting depth, hydraulic characteristics) and seasonal variation in soil N content should be a priority to further our understanding of diversity effects on productivity and potential limiting resources in this ecosystem. Furthermore, if more diverse plant assemblages used available soil N forms more completely, one should also expect to observe reduced ammonium and nitrate concentrations in the rooting zone of these plots (Hooper & Vitousek, 1997; Spehn et al., 2005). Yet, contrary to previous work (Palmborg et al., 2005; Roscher et al., 2008; Tilman et al., 1996), functional diversity did not significantly change the predominant N form concentrations (i.e. nitrate) at our site (Figure S8).

Overall, we found evidence that more productive and species-rich communities have higher N uptake and photosynthesis, suggesting that these two physiological processes could, among other mechanisms, have contributed to the enhanced AP. However, as N demand and photosynthesis are also likely to be higher in communities with higher biomass, the causal links between AP and N uptake are challenging to decipher in this experiment. Especially as we did not find an increase in N uptake per gram of biomass with increasing SR. It is therefore not clear if plots with higher biomass took up more N because their demand was higher or if the higher uptake of N was the driver of higher biomass production. Multiple seasonal measurements of soil N availability, plant N uptake and soil microbial composition would be needed to understand better the link between soil biogeochemistry, leaf physiology and productivity in these systems.

Contrary to our expectations and to previous work (Gubsch et al., 2011; Poorter & De Jong, 1999), our results show that functional composition had little impact on productivity and N uptake (Figures 1c and 2c; Table 1). Like other studies conducted in experimental grasslands (e.g. Roscher et al., 2012; Zhang et al., 2017), we defined functional composition using community-weighted mean traits. However, we focussed on one trait (SLA) that is a key indicator of the resource economic spectrum and is manipulated in the experiment. We would expect that fast-growing high SLA communities should be more productive as they are better at rapidly acquiring resources (e.g. Lavorel & Grigulis, 2012). The lack of an effect of SLA on productivity might indicate that fast-growing species are limited by other resources (e.g. phosphorus or water) and do not reach their maximum growth rates in this system. This could also potentially explain the reduced photosynthetic rates observed with increasing SLA (Figure 3c). Alternatively, leaf anatomical adjustments, including higher investment in mesophyll tissues relative to epidermis and cuticles in low SLA species could contribute to this pattern (e.g. Gonzalez-Paleo & Ravetta, 2018; Niinemets, 1999). However, communities composed mainly of high SLA species had lower soil ammonium concentrations (Table 1; Figure S8c), which could be associated with a higher ammonium uptake of fast-growing species, as previously observed in tree species (Miller & Hawkins, 2007).

Although fertilization increased AP, N uptake and soil ammonium concentration (Table 1), it did not alter the impact of SR, functional

diversity and composition on community-level carbon and N relations in the soil and vegetation. Where positive effects of SR were found (i.e. increased productivity, N uptake and photosynthesis), N enrichment through fertilizer did not amplify or cancel these effects. This finding is similar to the results of Craven et al. (2016) who conducted a meta-analysis using data from 16 grassland experiments and observed that soil nutrient alterations did not change biodiversity–ecosystem functioning relationships. Together with the lack of effect of functional diversity on N uptake, this result suggests that nutrient use complementarity for N is unlikely to explain the positive effect of SR on productivity. The lack of an interaction between N addition and SR also suggests that diversity effects are consistent along fertility gradients and that increasing SR could also boost productivity in fertile conditions, for example in an agricultural context (Li et al., 2020).

4.2 | Impact of diversity, functional composition and fertilization on water use efficiency

The direct effect of fertilization on $\delta^{13}C$ indicates that N addition increased water use efficiency (Table 1), and thus that plants probably faced increased soil moisture stress when fertilized. Several underlying processes could be driving this response including increased above-ground biomass production and reduced below-ground investment (i.e. higher shoot:root ratio), leading to higher water consumption and exacerbated stress, particularly in extreme moisture-limited conditions (Klaus et al., 2020). Indeed, we found a lower water content in fertilized plots, but no effect of AP on $\delta^{13}C$ (Figure S6). These findings highlight the urgent need to move towards alternative management solutions that reduce the excessive use of fertilizer to maintain the productivity and drought tolerance of grasslands in a rapidly changing climate.

Sustainable management approaches could include manipulation of SR and species composition. Indeed, the significant reduction in $\delta^{13}C$ with increasing SR at low to intermediate CWM_{SLA} (Figure 4a) implies that plot-level water availability was enhanced in communities dominated by slow-growing species and communities with mixed traits, independently of fertilization levels. These findings are consistent with our expectations and with previous work finding positive effects of diversity on resistance to drought (e.g. Cole et al., 2019; Guderle et al., 2017; Isbell et al., 2015; Kreyling et al., 2017; Tilman & Downing, 1994). However, the effect of SR on $\delta^{13}C$ was opposite for communities dominated by fast-growing species. The underlying mechanisms driving lower $\delta^{13}C$ in plots with high SR could be below-ground niche partitioning and facilitation processes such as root stratification, hydraulic redistribution and/ or higher functional diversity of the fungal community (Verheyen et al., 2008). Additionally, species-rich assemblages are more productive and may provide greater shade, cooler air temperature, lower atmospheric evaporative demand and higher soil moisture availability (Cappelli et al., 2020; Cowles et al., 2016; Steinauer et al., 2015). Indeed, the significant positive effect of bare ground cover on $\delta^{13}C$ suggests that as conditions become drier, higher biomass (and thus

lower bare ground cover) reduces drought stress, and thus reduces water use efficiency (Figure 4c). We did not find an effect of functional diversity on $\delta^{13}C$ (Figure 4b), suggesting that complementarity in leaf economic traits is not a key driver of water use efficiency and that a diversity in different traits is likely important. Future work should focus on collecting hydraulic traits associated with drought strategies (e.g. isohydricity, water uptake depth, rooting structure) to compile new functional diversity indices and understand the mechanistic drivers of reduced water use efficiency in species-rich communities. Furthermore, $\delta^{13}C$ results should be interpreted with care as other factors, particularly shading in more productive plots could reduce photosynthesis rates, resulting in reduced $\delta^{13}C$ (Farquhar et al., 1989). However, as we found higher photosynthesis in species-rich plots (Figure 3a), we do not expect this confounding effect to strongly influence our findings.

We further expected slow-growing communities, which often have lower plant growth rates and reduced water use (e.g. Mariotte et al., 2013; Reich et al., 1999), to be less subjected to restricted water supply than fast-growing communities (Craven et al., 2018). Indeed, a strong effect of functional composition was observed with more negative $\delta^{13}C$ (suggesting lower water use efficiency and drought exposure) in plots with lower CWM_{SLA} (Figure 4a). Interestingly, no interaction between functional composition or diversity and the water balance was found. Thus, reduced water use efficiency in species-rich and slow-growing species plots was consistently maintained across years, even though species experienced different stress intensities. These findings support observations from Craven et al. (2016) where in 16 different experimental grasslands across North America and Europe, diversity effects on AP were independent of reductions in water availability. Our findings thus indicate that interaction mechanisms such as complementarity and facilitation for water resources could dominate diversity effects on water use efficiency at this site, independently of soil moisture conditions.

5 | CONCLUSIONS

Our study provides strong evidence that high SR increases plant N uptake, photosynthesis and productivity, and reduces water use efficiency in slow- to intermediate-growing communities in temperate grasslands, highlighting that biodiversity is of tremendous importance in driving ecosystem properties. Hence, favouring and conserving high SR could provide an option to effectively maintain the high productivity of grasslands while promoting stronger stability against extreme climatic events. Nevertheless, our work also showed that certain monocultures or low-species mixtures can still have higher productivity than mixtures of 20 species. However, previous work has shown that although low diversity communities may produce high biomass in particular years, they are not able to produce consistently high biomass across time (Allan et al., 2011; Tilman et al., 2006). Furthermore, our work highlighted that different community characteristics drive particular ecosystem processes but that no process is enhanced by all of them. In general, both functional

composition and sown SR altered grassland water use efficiency, but only SR significantly influenced biomass production and N uptake. Similarly, we did not find functional diversity in leaf economic traits increasing N uptake, carbon uptake or water use efficiency. Thus, one may expect that other traits, perhaps hydraulic ones, are more important drivers of plant water use, N uptake and ecosystem water use efficiency. While fertilization apparently increases productivity, it also leads to increased water use efficiency, and thus higher drought stress during unfavourable conditions. These findings are fundamental for our understanding of N deposition effects and highlight the urgent need for a more sustainable N fertilizer application in agroecosystems and a switch to lower input in higher diversity systems in order to better tolerate future climate changes.

CONFLICT OF INTEREST

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

AUTHORS' CONTRIBUTIONS

C.G., A.G. and E.A. conceived the study and designed the methodology; M.W., E.A., M.D.-G., M.M.L., S.L.C., N.A.P. and C.G. conducted the fieldwork; M.W. analysed the data; M.W. and C.G. led the manuscript writing, and all authors contributed to the drafts and gave their final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data used in this manuscript are archived with Dryad Digital Repository: https://doi.org/10.5061/dryad.0cfxpnw31 (Grossiord et al., 2021).

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SUPPORTING INFORMATION

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