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Species richness promotes ecosystem carbon storage: evidence from biodiversity-ecosystem functioning experiments

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Plant diversity has a strong impact on a plethora of ecosystem functions and services, especially ecosystem carbon (C) storage. However, the potential context-dependency of biodiversity effects across ecosystem types, environmental conditions and carbon pools remains largely unknown. In this study, we performed a meta-analysis by collecting data from 95 biodiversity-ecosystem functioning (BEF) studies across 60 sites to explore the effects of plant diversity on different C pools, including aboveground and belowground plant biomass, soil microbial biomass C and soil C content across different ecosystem types. The results showed that ecosystem C storage was significantly enhanced by plant diversity, with stronger effects on aboveground biomass than on soil C content. Moreover, the response magnitudes of ecosystem C storage increased with the level of species richness and experimental duration across all ecosystems. The effects of plant diversity were more pronounced in grasslands than in forests. Furthermore, the effects of plant diversity on belowground plant biomass increased with aridity index in grasslands and forests, suggesting that climate change might modulate biodiversity effects, which are stronger under wetter conditions but weaker under more arid conditions. Taken together, these results provide novel insights into the important role of plant diversity in ecosystem C storage across critical C pools, ecosystem types and environmental contexts.

1. Introduction

Plant diversity has been shown to have a strong positive impact on ecosystem functioning and service provisioning [1–3]. Plant diversity loss due to global change and land-use change [4,5] can threaten ecosystem functioning [6,7], whereas restoration of plant diversity, such as afforestation of mixed forests, can increase ecosystem functioning [8,9]. To explore the causal relationship between plant diversity and ecosystem functioning, a series of plant biodiversity-ecosystem functioning (BEF) studies, distributed across different ecosystem types and experimental durations, have emerged since the mid-1990s [10,11]. These BEF studies have paid much attention to ecosystem
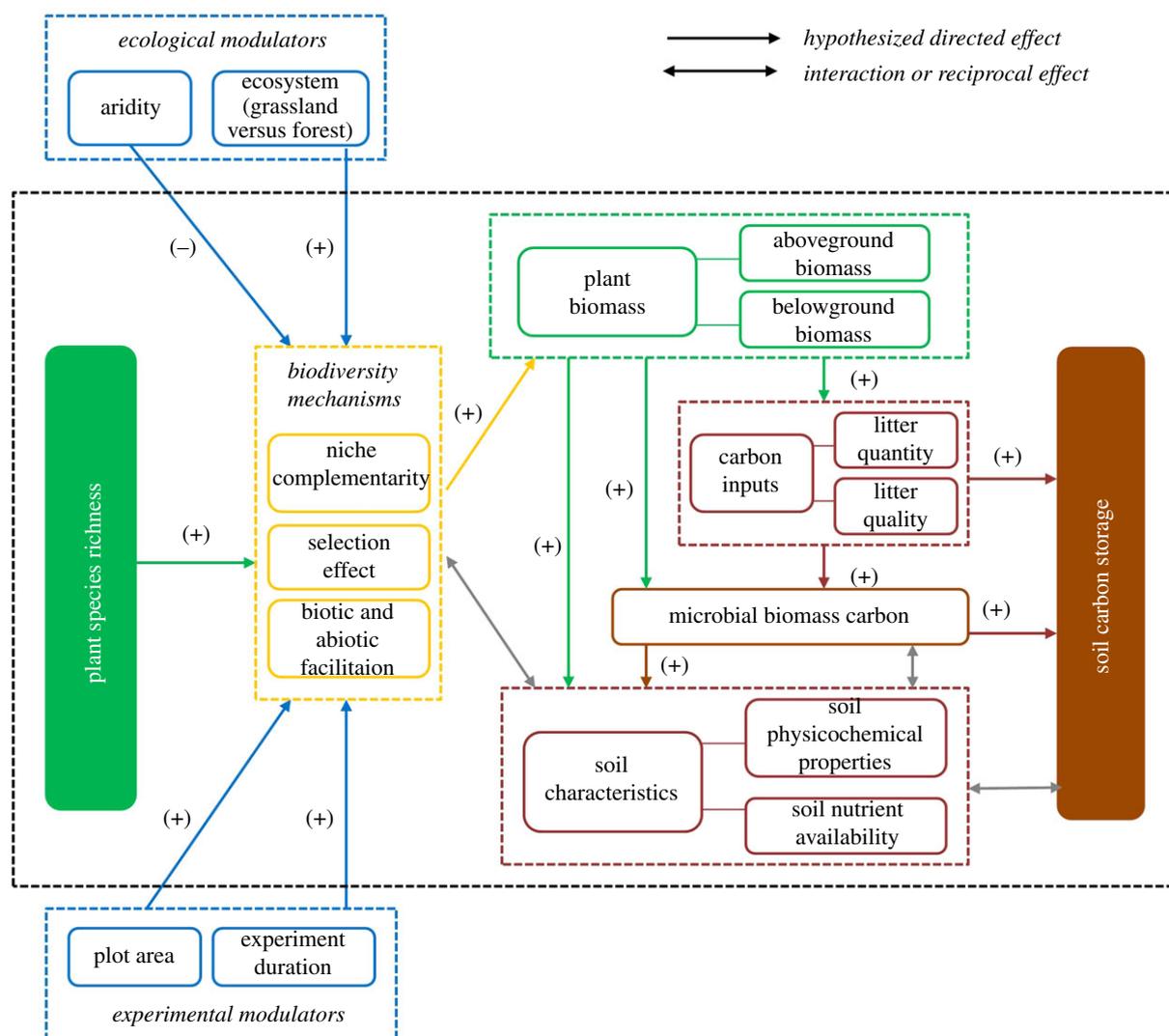
Figure 1. Conceptual model for the potential relationships between plant species richness, carbon pools, and different ecological and experimental modulators. (+): positive effect; (−): negative effect. (Online version in colour.)

carbon (C) storage, including both above- and belowground C storage, often indicated by plant biomass and soil C storage [12–14] (figure 1). Although many of these experiments found compelling empirical evidence for the positive relationships between plant diversity and plant productivity as well as soil C stocks [9,12,15], there is still much uncertainty about the plant diversity–ecosystem C storage relationship. For example, it is still unclear whether plant biomass and soil C storage respond consistently to plant species richness; whether plant diversity–ecosystem C storage relationships are consistent across multiple ecosystem types; and how plant diversity–ecosystem C storage relationships change with experimental duration. All of these uncertainties call for a quantitative and comprehensive synthesis based on these BEF studies, which is critical to determine ecosystem functioning that is susceptible to changes in plant diversity.

Plant biomass, including above- and belowground biomass, represents an important ecosystem C pool. Large numbers of studies have found that plant diversity has a positive effect on plant productivity, which is attributed to the major mechanisms of interactions among plant species and environmental filters, such as competition reduction, niche complementarity, selection effects, and biotic and abiotic facilitation under high plant diversity (as depicted in the conceptual model in figure 1) [16–18]. In addition, much attention has been

focused on whether both above- and belowground biomass increase with plant diversity, and how the allocation of above- and belowground biomass changes with plant diversity [19,20]. Given that plant growth is distinct among biomes and regulated by climate conditions, the environmental modulators, such as ecosystem types (i.e. forest, grassland and wetland etc.) and climate conditions (such as aridity), can affect the relationship between plant diversity and plant biomass production [3] (figure 1). The stress gradient hypothesis suggests that competitive interactions may be more pronounced under very beneficial environmental conditions, while facilitative interactions and complementarity may dominate in harsh environmental conditions [21]. However, evidence from BEF experiments is mixed (e.g. [22,23]), and some studies suggest that biodiversity effects increase under high resource supply [24,25]. Resulting stronger biodiversity effects under more moist and nutrient-rich conditions may further differ between C pools, as high soil resource availability may enhance aboveground biomass production more than belowground biomass production. Moreover, the strength of the BEF relationship [26,27], as well as the underlying mechanisms related to environmental regulation [28] may be scale-dependent, therefore the plot area of BEF experiments can also affect ecosystem responses to species richness (figure 1). Synthesis and theoretical work suggest that biodiversity effects

on ecosystem functioning may increase with spatial scale due to multiple non-exclusive mechanisms like covering more environmental conditions [28,29]. However, how this may translate into changes across different C pools has not been explored. In addition to these spatial considerations, the response magnitude of C pools to species richness may become stronger with experimental duration (figure 1), as some ecological mechanisms might need many years to materialize [14,30,31]. These effects of ecological and experimental modulators on the plant diversity–productivity relationship cannot be clarified in case studies of BEF experiments, which needs a synthesis of data from BEF studies.

Globally, the soil C pool is larger than the atmospheric C pool and vegetation C pool together [32]. Plant diversity is likely to promote soil C storage by increasing plant C inputs and stimulating soil microbial activity [12,33,34]. There is mounting empirical evidence for a positive relationship between plant diversity and soil microbial activity [12,14,35], which can, in turn, promote the processing of plant-derived resources [36], accumulation of soil microbial necromass, and thus an increase in soil C content [37,38] (figure 1). Apart from the quantity of plant C inputs, higher quality (as indicated by e.g. higher litter nitrogen (N) content, lower litter C to N ratio, lower litter lignin content) and diversity of plant-derived inputs at high plant diversity may contribute to governing soil C accumulation [12,36,39]. In addition to biotic effects, beneficial abiotic environments in diverse plant communities, such as higher soil moisture and neutral soil pH, can contribute to explaining the positive relationship between plant diversity and soil C storage [40,41]. However, plant diversity, potentially triggering a large diversity of decomposers, can also increase soil respiration [14]. Therefore, soil C dynamics and accumulation are affected indirectly by plant diversity due to the variations in the quantity and quality of litter inputs, microbial activity, and the abiotic environment of decomposition under high plant diversity (figure 1). These imply that plant diversity effects on soil C accumulation can be context-dependent and vary across ecosystem types, plot sizes, climatic conditions and change over the course of an experiment [12,42].

Some meta-analyses have summarized the respective effects of plant diversity on plant productivity, soil microbial biomass or soil C storage [43–45]. However, several of them have mixed observational studies of natural plant diversity gradients with BEF experiments, as well as focused on a certain ecosystem type. In addition, there is still much uncertainty regarding the relative response magnitude of different C pools to plant diversity. Therefore, a comprehensive and quantitative synthesis of the relationship of plant diversity to ecosystem C storage and its ecological and environmental modulators based on BEF studies is urgently needed. To address these critical knowledge gaps, we performed a meta-analysis by collecting the data from 95 BEF studies at 60 sites to clarify how plant species richness promotes ecosystem C storage across different C pools (including aboveground biomass, belowground biomass, microbial biomass C and soil C storage), ecosystem types, as well as spatial and temporal scales. We tested the following hypotheses as depicted in the conceptual model (figure 1):

(H1) Plant species richness promotes ecosystem C storage, including the critical C pools of aboveground and belowground biomass, microbial biomass C and soil C content, and their response magnitudes will be enhanced by increasing levels of species richness.

(H2) Plant diversity increases plant growth and soil C accumulation by creating more favourable soil characteristics, such as neutral soil pH, increased soil moisture and nutrient content, and thus promotes ecosystem C storage.

(H3) Given plant growth and ecosystem C cycling can be affected by the spatio-temporal factors, we hypothesize that the relationship of plant diversity–ecosystem C storage can be regulated by both experimental modulators (i.e. BEF relationships are expected to increase with plot size and experimental duration) and ecological modulators (such as ecosystem types and climate, represented by aridity index; i.e. BEF relationships are expected to decrease under more arid conditions).

2. Methods

(a) Data collection

From February to June in 2020, we conducted a comprehensive search of relevant peer-reviewed articles and dissertations published from the year of 1990 to 2020 (given that plant BEF studies have emerged since around the mid-1990s) in the Web of Science and ProQuest databases using combinations of the following search string: (plant 'diversity' OR 'biodiversity' OR 'tree diversity' OR 'species diversity' OR 'plant species richness' OR 'species mixture' OR 'plant community composition') AND ('plant growth' OR 'plant productivity' OR 'plant biomass' OR 'basal area') AND ('soil microbial*' OR 'soil biota' OR 'soil bacterial and fungal*') AND ('soil carbon' OR 'soil organic carbon'). We then cross-checked the references of the relevant articles to identify other relevant book chapters and peer-reviewed reports. According to the search string, we initially obtained nearly 200 relevant papers from thousands of appearing papers. We then excluded the papers that were natural diversity gradient studies (e.g. [39]), controlled global change experiments, in which plant diversity has been altered by global change factors, but not having a direct diversity treatment (e.g. [46]), meta-analysis studies (e.g. [45]) or review studies (e.g. [47]), and the papers not including C storage and other variables that were in the focus of this study. We kept the papers from BEF experiments and experiments that had one-species and mixed-species plantations. Finally, we used data from 95 BEF studies across 60 sites (with the earliest study being published in 1997).

We extracted data for the following variables. (a) Soil respiration (i.e. soil CO_2 emission), which included both microbial respiration and autotrophic respiration, and total soil carbon or soil organic carbon (given as % or $g\,kg^{-1}$) in topsoil (i.e. the upper 20 cm of mineral soil). In the literature used for data collection, most studies provided data on soil C content ($g\,kg^{-1}$ or %), not soil C stock ($g\,m^{-2}$ or $kg\,ha^{-1}$). In addition, only two studies provided data on soil bulk density. Therefore, in this study, we used soil C content data to represent soil C storage, and we did not use the limited data on bulk density. (b) Plant biomass, including aboveground biomass ($g\,m^{-2}$) or basal area ($m^2\,ha^{-1}$), belowground biomass, or fine root biomass from soil cores or in-growth soil cores ($g\,m^{-2}$). (c) Microbial properties, including heterotrophic respiration or microbial respiration, which reflected microbial activities, microbial biomass carbon ($mg\,kg^{-1}$). (d) Soil physico-chemical properties, including soil pH, soil moisture (%), soil NH_4^+ and NO_3^- concentration ($mg\,kg^{-1}$), soil C to N ratio (soil C/N ratio). (e) Litter decomposition rate, including litter N content, litter C/N ratio, litter decomposition rate (k). (f) Soil microbial communities, including fungal phospholipid fatty acids (PLFAs), bacterial PLFAs, fungal to bacterial biomass ratio (F to B ratio), Gram+ PLFAs, Gram− PLFAs and Gram+ to Gram− ratio. In our study, we indicated ecosystem C storage as aboveground plant biomass, belowground plant biomass, microbial biomass C
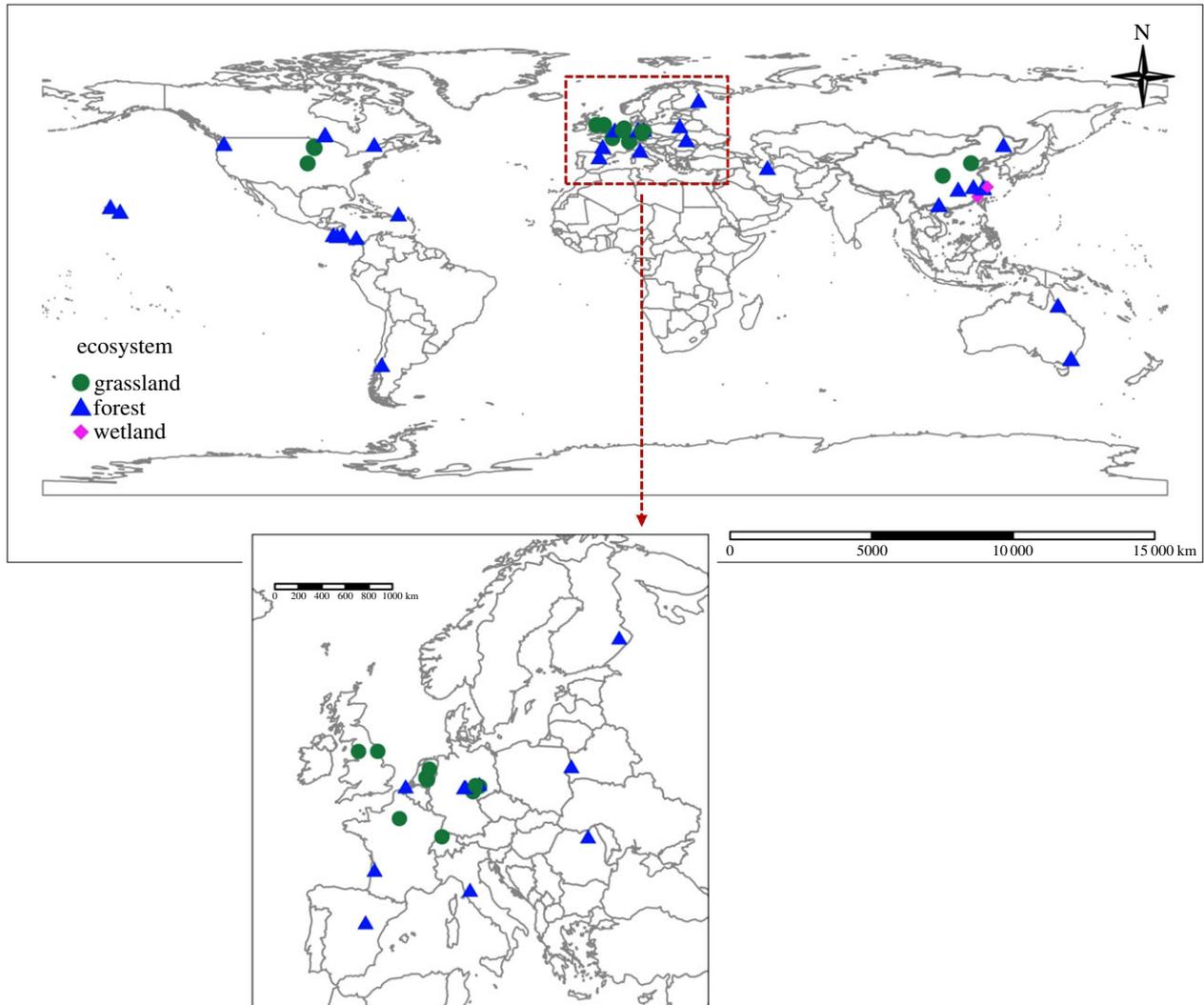
Figure 2. The distribution of sites across all ecosystems. Green circles represent grassland, blue triangles represent forest and pink diamonds represent wetland. (Online version in colour.)

and soil C content. We also extracted data for site information, including latitude and longitude of the site, mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), ecosystem types, plant species richness, plot area (m²) and experimental duration (number of years).

We converted all soil C content data to the same unit (g kg⁻¹). We collated data from the main texts, tables and figures. The numerical values from graphically presented data were extracted by digitizing the figures using Engauge Digitizer (Free Software Foundation, Boston, USA). We included datasets from multiple years or experimental levels, but from the same sites. We are aware of the fact that there is a lack of non-independence of observations when including several observations from one study or/ and site. However, the proportion of dependent observations varied substantially across response variables but never exceeded 50% (all sites: 36% of the 94 studies across 60 sites; aboveground biomass: 41% of 34 studies across 20 sites; belowground biomass: 4% of 24 studies across 23 sites; microbial biomass C: 48% of 25 studies across 13 sites; soil C: 25% of 24 studies across 18 sites). To control for the existing non-independence, the factors 'study' and 'site' were used as random factors in the analyses to account for the non-independence of data coming from the same study. Finally, we got 191 pairs of data for aboveground biomass, 111 pairs of data for belowground biomass, 94 pairs of data for microbial biomass C and 131 pairs of data for soil C content. In addition, we got 418 pairs of data for other variables. In total, we got 945 pairs of data in this study.

The spatial range of the sites included in our study was from 40.13 S to 62.6 N, and from 158.33 W to 149.25 E. The ecosystems in our dataset included grassland, wetland, plantation, temperate forest, and subtropical and tropical forest. We grouped plantation, temperate forest, and subtropical and tropical forest together as forest. Therefore, we divided the ecosystems into three types: grassland, forest and wetland. However, most of our analyses and discussion focused on grassland and forest due to limited data availability for wetlands (four studies at two sites). The distribution of the experimental sites included in our study are shown in figure 2, which were generated by using the packages tmap [48] in R. Detailed information of the studies included in the meta-analysis is provided in electronic supplementary material, table S2.

(b) Meta-analysis

The data were analysed using effect sizes for each observation calculated as the natural log of the response ratio (RR): $RR = \ln(\overline{X_t}/\overline{X_c})$, where $\overline{X_c}$ is the control mean (i.e. data from one species plots) and $\overline{X_t}$ is the treatment mean (i.e. data from multiple species plots [49]; hereafter called species richness treatment). Thus, there is only one control (i.e. one-species/monoculture plots), but probably multiple treatment variations due to multiple levels of species richness treatments (e.g. 3, 6, 9 species), which means we calculated multiple LnRRs from one study. We controlled for this non-independence of observations by using study (and site) as random factor. Effect sizes and variances were calculated using

random-effects models (with restricted maximum-likelihood estimators), as these, in addition to sampling error, allow for cross-study variability in true effect sizes [50,51]. The effect was significantly different from zero, if 95% confidence intervals did not overlap with zero. We ran standard meta-analyses and tested the total heterogeneity of effect sizes within each model. Significant p-values ($p < 0.05$) indicated heterogeneity in effects between studies when accounting for sampling error [52]. To identify differences in the magnitude of effects among ecosystem types, we conducted a subgroup analysis for each parameter. We present results for separate ecosystems only where at least three observations were available in more than one subgroup. However, the results were considered valid, when there were at least four observations [53]. Total heterogeneity (Q_T) was partitioned into within-group (Q_W) and between-group (Q_B) heterogeneities, whereby a significant Q_B indicates significant differences among groups [49]. Group means were considered significantly different if their 95% confidence intervals did not overlap. The publication bias was estimated by the dnorm function (electronic supplementary material, figure S1), and the frequency distributions of all the RR values for the target variables followed a normal distribution, indicating an absence of publication bias in our study [54]. We used study ID nested in site ID (site/study) as random factor in each of the models to account for the dependence of observations originating from the same study. All statistical analyses were conducted with the 'metafor' package [55] in R to test our hypotheses H1 and H2.

(c) Aridity index

An unfavourable abiotic environment, such as drought, is not beneficial for plant growth, which will affect the development of the plant community. Thus, the level of climate aridity has been found to be the most important factor in regulating the relationship between plant species richness and community biomass [56]. To compare the level of climate aridity among sites, we used the De Martonne aridity index (AI) [57,58], which was calculated for each site as follows:

$$AI = \frac{MAP}{MAT + 10},$$ (2.1)

where MAP is mean annual precipitation, and MAT is mean annual temperature. Lower aridity index values correspond to more arid conditions, whereas higher values correspond to a more humid climate.

(d) Other statistical analyses

To further examine the effects of plant species richness level on the changes in plant biomass, microbial biomass and soil C content, we performed linear and nonlinear regressions (polynomial relationships) between plant species richness and the response magnitudes of the four C pools. This method was used to test our hypothesis H1. We also used linear and nonlinear regressions to analyse the correlations of the response magnitude of the four C pools with aridity index, plot area and experimental duration. This method was used to test our hypothesis H3.

We used linear mixed models to further analyse how the three factors, i.e. climate (indicated by aridity index), plot area and experimental duration, affect the diversity–ecosystem C storage relationship, in which species richness, aridity index, experimental duration and plot area acted as fixed factors, whereas ecosystem type and site acted as random factors. We used the R package 'lme4' [59] to fit linear mixed-effects models and used 'lmerTest' [60] to calculate Satterthwaite approximations of p-values. This part aimed to test our hypothesis H3.

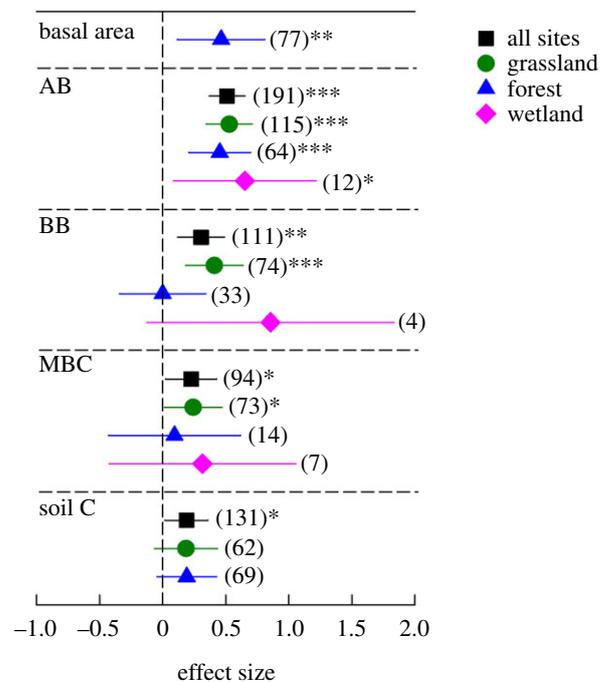All these analyses were conducted in R (https://www.R-project.org/).

Figure 3. The effects of plant species richness on basal area, aboveground biomass (AB), belowground biomass (BB), microbial biomass carbon (MBC) and soil carbon (Soil C) content across all ecosystems, in grassland, forest and wetland. Black squares represent data from all sites, green circles represent data from grassland, blue triangles represent data from forest and pink diamonds represent data from wetland. Effect sizes are shown as natural log-response ratios for n studies per response variable. Confidence intervals of an effect size overlapping zero (dashed line) indicates no change relative to controls, whereas effects are significant when confidence intervals do not overlap with zero (indicated by asterisks, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Numbers in parentheses represent the number of observations for each parameter. (Online version in colour.)

3. Results

(a) The effect of plant species richness on ecosystem C storage

In our study, we indicated ecosystem C storage as aboveground plant biomass, belowground plant biomass, microbial biomass C and soil C content. Our meta-analysis results showed that, overall, high plant species richness significantly increased aboveground biomass ($+51\% \pm 14\%$), belowground biomass ($+30\% \pm 19\%$), microbial biomass C ($+23\% \pm 20\%$) and soil C content ($+19\% \pm 17\%$) (figure 3). When data were divided into different ecosystems, we found that there were significant differences between the responses of belowground biomass and microbial biomass C to higher plant diversity in grassland and forest, with significant increases in grassland but no significant change in forest (figure 3). However, no differences were found in the responses of aboveground biomass and soil C content to increased plant diversity between grassland and forest (figure 3). For wetland, aboveground biomass was significantly increased by plant species richness, but belowground biomass and microbial biomass C did not change significantly (figure 3). For forest, where some studies provided data on basal area instead of aboveground biomass, we found that basal area was significantly increased by increased plant diversity ($+46\% \pm 35\%$) (figure 3).

In our dataset, relatively few studies presented data for the four C pools simultaneously. To test whether plant diversity
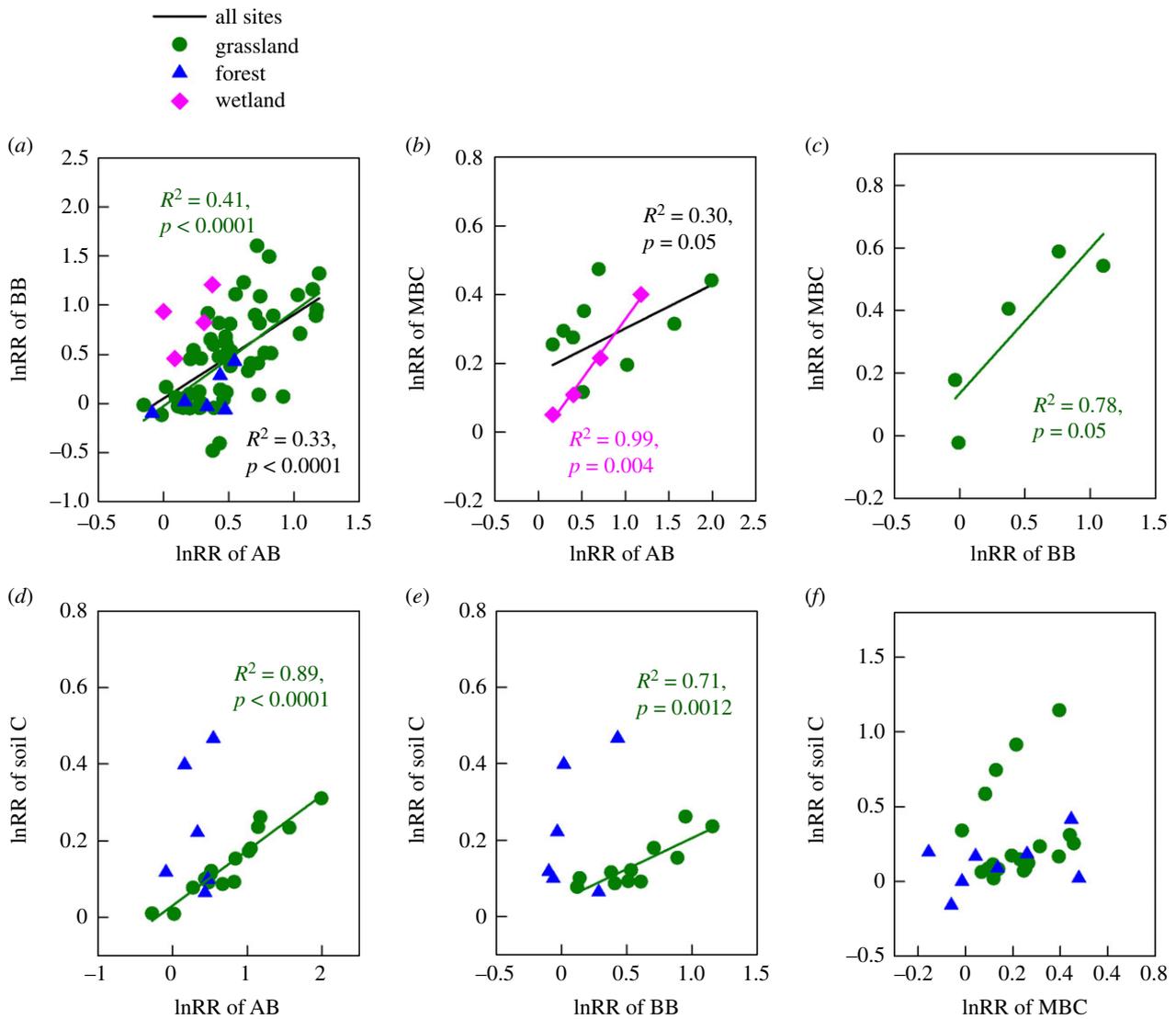
Figure 4. The pair-wise relationships among the response ratios of the four variables aboveground biomass (AB), belowground biomass (BB), microbial biomass carbon (MBC) and soil carbon (soil C) content in grassland, forest and wetland: (a) AB versus BB, (b) AB versus MBC, (c) BB versus MBC, (d) AB versus soil C, (e) BB versus soil C and (f) MBC versus soil C. Green circles represent data from grassland; blue triangles represent data from forest; and pink diamonds represent data from wetland. The black line represents the linear regression line across all ecosystems, the green line represents the linear regression line in grassland, whereas the pink line represents the linear regression line in wetland. Regression lines are shown for significant relationships (p < 0.05). (Online version in colour.)

leads to an increase in one pool, but a decrease in another, i.e. shifts in C allocation, we used the subdataset that included data of at least two C pools in one study to analyse their pair-wise relationships. Across all ecosystems, the positive correlations between lnRRs of AB versus BB ($R^2 = 0.33$, $p < 0.0001$) and AB versus MBC ($R^2 = 0.30$, $p = 0.05$) were significant (figure 4a,b). For grassland, we found positive correlations between the lnRRs of AB versus BB ($R^2 = 0.41$, $p < 0.0001$), BB versus MBC ($R^2 = 0.78$, $p = 0.05$), AB versus soil C ($R^2 = 0.89$, $p < 0.0001$) and BB versus soil C ($R^2 = 0.71$, $p = 0.0012$; figure 4a,c,d,e). For forest, no significant correlations were found; whereas for wetland, only the correlation of lnRR of AB versus MBC was significant ($R^2 = 0.99$, $p = 0.004$; figure 4b).

In addition, we observed that the level of species richness affected the response magnitude of all four C pools (figure 5). Across all ecosystems, the response magnitude of aboveground biomass increased with species richness at low levels of plant diversity, but then decreased at around 20 species ($R^2 = 0.14$, $p < 0.0001$; figure 5a). It should be noted that the number of data points with more than 20 species is only 2 for aboveground biomass (figure 5a), and the respective results should thus be

interpreted with caution. The response magnitude of microbial biomass C also followed the same trend with aboveground biomass ($R^2 = 0.23$, $p = 0.0004$, figure 5c). However, the response magnitudes of belowground biomass ($R^2 = 0.11$, $p = 0.0047$) and soil C content ($R^2 = 0.23$, $p < 0.0001$) increased linearly with the level of species richness (figure 5b,d). The reader should note though that the highest diversity levels for aboveground biomass, belowground biomass, microbial biomass C and soil C content were 16, 16, 16 and 60 species, respectively (figure 5a–d). The same patterns were also observed for aboveground biomass ($R^2 = 0.26$, $p < 0.0001$), belowground biomass ($R^2 = 0.11$, $p = 0.0047$), microbial biomass C ($R^2 = 0.23$, $p = 0.0004$) and soil C content ($R^2 = 0.23$, $p < 0.0001$) in grassland (figure 5a–d).

(b) Factors modulating the response magnitude of ecosystem C storage to plant species richness

We used both linear regressions and linear mixed-effects models to analyse the correlations between species richness and the response magnitudes of the four C pools, as well
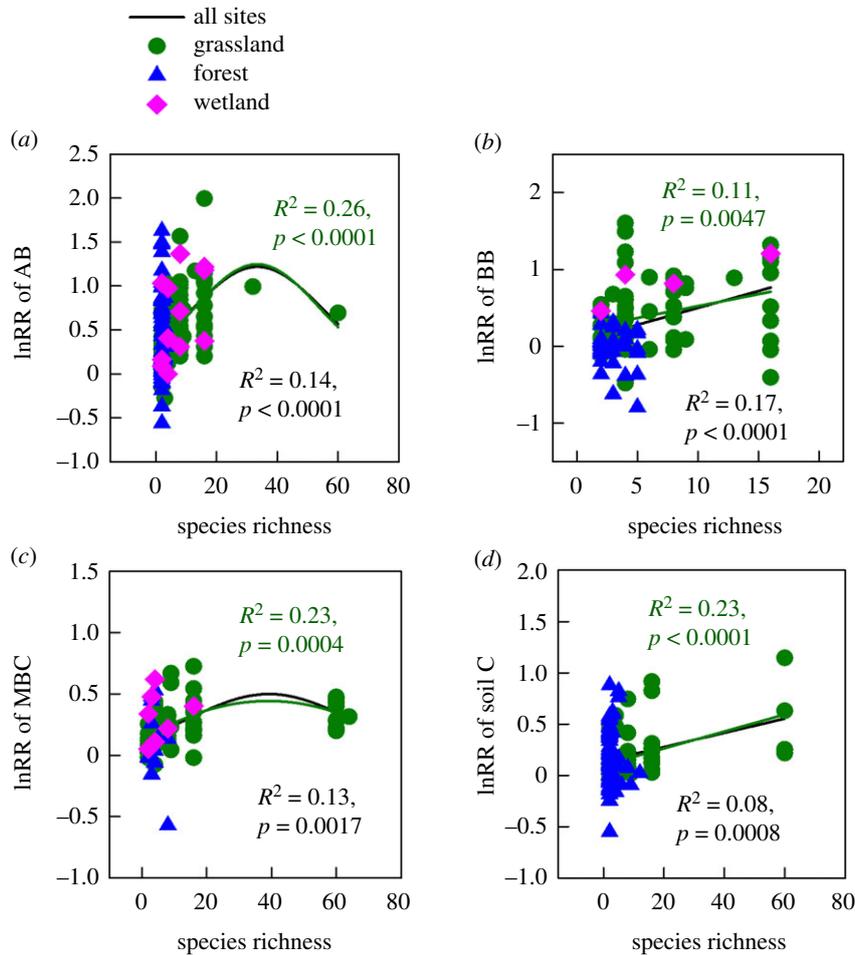
Figure 5. Relationships between plant species richness and the response magnitude (LnRR) of (*a*) aboveground biomass (AB), (*b*) belowground biomass (BB), (*c*) microbial biomass carbon (MBC), (*d*) as well as soil carbon (soil C) content across all ecosystems. Green circles represent data from grassland; blue triangles represent data from forest; and pink diamonds represent data from wetland. The black line represents the linear regression line across all ecosystems, whereas the green line represents the linear regression line in grassland. The relationships were significant when $p < 0.05$. No significant relationships were found in forest and wetland. (Online version in colour.)

as the modulating factors (table 1 and figures 5 and 6). The linear regressions suggested that only the response magnitude of belowground biomass was affected by aridity index both in grassland ($R^2 = 0.08$, $p = 0.02$) and forest ($R^2 = 0.13$, $p = 0.06$; figure 6*b*); whereas the response magnitudes of aboveground biomass, microbial biomass C and soil C content were not affected by aridity index across ecosystems or in a specific ecosystem (figure 6*a,c,d*). The response magnitude of aboveground biomass in grassland decreased with plot area ($R^2 = 0.05$, $p = 0.02$), and the response magnitude of belowground biomass decreased with plot area across ecosystems ($R^2 = 0.21$, $p < 0.0001$; figure 6*e,f*). However, the response magnitudes of microbial biomass C and soil C content were not affected by plot area (figure 6*g,h*).

In addition, the linear regressions suggested that, overall, the response magnitudes of aboveground biomass ($R^2 = 0.06$, $p = 0.0006$), belowground biomass ($R^2 = 0.07$, $p = 0.01$), microbial biomass C ($R^2 = 0.10$, $p = 0.0024$) and soil C content ($R^2 = 0.04$, $p = 0.04$) slightly increased with experimental duration across all ecosystems (figure 6*i–l*). For grassland, the response magnitudes of aboveground biomass ($R^2 = 0.29$, $p < 0.0001$), belowground biomass ($R^2 = 0.14$, $p = 0.0011$), microbial biomass C ($R^2 = 0.20$, $p < 0.0001$) and soil C content ($R^2 = 0.08$, $p = 0.03$) increased significantly with experimental duration (figure 6*i–l*). The results from linear mixed-effects models also

suggested that experimental duration significantly positively modulated the relationship between species richness and the response of the four C pools (table 1).

(c) The effect of plant species richness on soil abiotic and biotic environment

We also collected data on the soil abiotic and biotic environment, including soil respiration, litter decomposition rate, soil moisture, soil pH, soil N and phosphorus (P) content and soil microbial communities. However, the responses of soil abiotic and biotic environment to plant diversity were not significant across ecosystems, as well as when analysed for grassland and forest separately (figure 7).

4. Discussion

In this study, we investigated how plant species richness affects ecosystem C storage in plant above- and belowground biomass, soil microbial biomass C and soil C content by collecting data from controlled plant diversity experiments (BEF studies) across different ecosystem types, as well as spatial and temporal scales. This meta-analysis provides strong empirical evidence that plant species richness significantly enhances ecosystem C

Table 1. Fixed and random effects of the linear mixed effects analyses for all dependent variables, i.e. aboveground biomass (AB), belowground biomass (BB), microbial biomass carbon (MBC) and soil carbon (C) content. Species richness is the independent variable. Aridity index, plot area and experimental duration acted as fixed factors, whereas ecosystem type and site acted as random factors. LnRR, the natural log of response ratio; SR, species richness; area, plot area; AI, aridity index; duration: experimental duration; site: experimental site; no. of observation: number of observation; std. dev, standard deviation; std. error, standard error. Significant results ($p < 0.05$) presented in italics.

variable	no. of observation	random factors	variance	std. dev.	fixed factors	estimate	std. error	*p*-value
AB	113	ecosystem	0.0009	0.0300	species richness	0.031	0.0054	*<0.0001*
		site	0.0037	0.0610	aridity index	0.002	0.0018	0.350
		residual	0.0840	0.2898	plot area	−0.001	0.0001	*0.007*
		—	—	—	experimental duration	0.033	0.0060	*<0.0001*
BB	81	ecosystem	0.0000	0.0000	species richness	0.030	0.0060	*<0.0001*
		site	0.3153	0.5615	aridity index	0.007	0.0170	0.672
		residual	0.0511	0.2260	plot area	−0.000	0.0002	0.503
		—	—	—	experimental duration	0.070	0.0115	*<0.0001*
MBC	89	ecosystem	0.0223	0.1492	species richness	0.0032	0.0010	*0.003*
		site	0.0101	0.1002	aridity index	0.0025	0.0018	0.194
		residual	0.02401	0.1549	plot area	-5.80×10^{-5}	9.96×10^{-5}	0.568
		—	—	—	experimental duration	0.0153	0.0047	*0.002*
soil C	114	ecosystem	2.80×10^{-8}	0.0002	species richness	0.0072	0.0028	*0.013*
		site	4.43×10^{-2}	0.2104	aridity index	-7.73×10^{-4}	0.0018	0.682
		residual	7.03×10^{-2}	0.2651	plot area	9.96×10^{-5}	8.55×10^{-5}	0.264
		—	—	—	experimental duration	0.0043	0.0035	0.230

storage, with stronger effects on aboveground biomass than on soil C content across environmental contexts and ecosystem types. Our study provided novel insights into the important role of plant diversity in ecosystem C storage and can contribute greatly to the field of BEF research.

(a) The effects of plant species richness on ecosystem C storage

Plant diversity plays an important role in ecosystem functioning and service provisioning, including ecosystem C storage [61,62]. Our study shows that the four major ecosystem C pools (above- and belowground biomass, microbial biomass C and soil C content) were significantly increased by plant species richness across all ecosystems (figure 3). In addition, the pair-wise correlations by the subdataset including data of at least two C pools were significantly positively correlated or non-significant (figure 4), which suggests that even if the allocation in the four C pools may be altered by plant diversity, high plant diversity will lead to a net increase in ecosystem C storage.

The mechanisms underlying the positive relationship of plant diversity and productivity are diverse, including competition reduction, niche complementarity, selection effects, and biotic and abiotic facilitation [16–18] (figure 1). Moreover, changes in soil physico-chemical properties and nutrient availability are also key mechanisms underlying the diversity–productivity relationship [63,64], which may have cascading effects on other C pools. Plant diversity can increase aboveground plant biomass and thereby also increase soil moisture by shading effects [34]. Moreover, plant diversity can increase soil moisture by enhancing soil aggregation with experimental

duration [65,66]. Plant diversity can also increase soil N concentrations and thus favour plant growth [67,68]. According to our results, soil moisture, soil NH_4^+ concentration and total soil N content tended to be increased at high plant diversity in comparison to monocultures, but these effects were not statistically significant (figure 7). Thus, the present work provides only limited support for the hypothesis that the physico-chemical environment in diverse plant communities favoured plant growth and thus enhanced plant biomass. However, we must also consider that these effects are site-specific and time-dependent [65,66]: there have been reports from some sites with a positive effect [69,70], whereas other sites observed non-significant or negative effects [17,70], which probably leads to the non-significant results in the meta-analysis. We also found soil P content to marginally increase at higher plant species richness across all ecosystems (figure 7), which also probably contributed to the increased plant productivity under high plant species richness. However, the reader should note that there was relatively fewer data on soil nutrients, particularly on soil P content, highlighting a potentially important research frontier for future plant diversity experiments by exploring changes in the storage and cycling of nutrients. In contrast to previous observations [36], we found that fungal biomass and F/B ratio were only slightly and non-significantly increased by higher plant species richness in grassland (figure 7). Thus, long-term studies are needed to explore if soil-borne fungi play an important role in regulating the plant diversity–productivity relationship [71].

Notably, when the data were partitioned into different ecosystems, we found that the responses of plant biomass differed between grassland and forest: although the magnitudes of the positive response of aboveground biomass to high
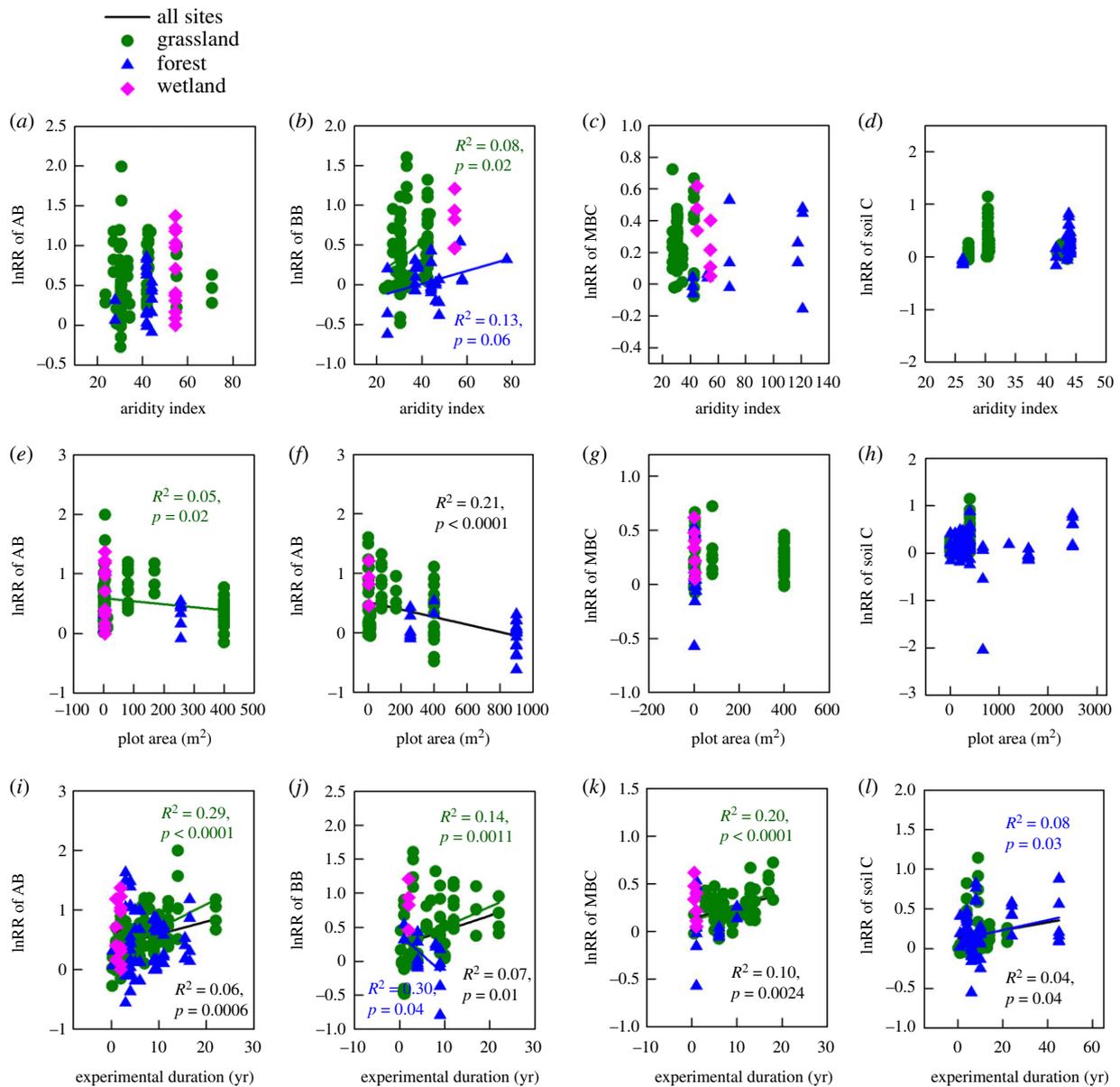
Figure 6. Relationships of LnRR of aboveground biomass (AB), belowground biomass (BB), microbial biomass carbon (MBC), as well as soil carbon (soil C) content and aridity index, plot area (m^2) and experimental duration (year) across all ecosystems. The green circle represents data from grassland, the blue triangle represents data from forest and the pink diamond represents data from wetland. The black line represents the linear regression line across all ecosystems, whereas the green line represents the linear regression line in grassland; and the blue line represents the linear regression line in forest. The relationships were significant when $p < 0.05$. (Online version in colour.)

plant diversity were not significantly different from each other, belowground biomass in grassland was significantly increased whereas belowground biomass in forest was not significantly altered by plant species richness (figure 3). Our study thus provided support for belowground overyielding in grassland [19], but not for forest. In addition, the pair-wise correlations by the sub-dataset including data of at least two C pools were significantly positive for grassland, but non-significant for forest (figure 4). These results suggest that ecosystem C pools in grassland were more responsive to high plant diversity than that in forest. In addition, the response magnitudes of the four C pools in grassland were more closely related to each other than those in forest. These results imply that the responses and mechanisms underlying plant diversity–ecosystem C pools in forest may be more complex compared to grassland. Future studies should focus more on plant diversity–productivity relationships in forest, because there was still a relatively low

number of BEF studies in forest ecosystems [64,72]. In this context, the TreeDivNet consortium [18,73,74] may be able to contribute important insights into BEF relationships, their context-dependency, and underlying mechanisms.

In addition, we found that the response magnitudes (the natural log of response ratio) of basal area, aboveground biomass and belowground biomass were influenced by the levels of species richness (2 species, 3–5 species, 6–9 species, 13–16 species and, greater than 16 species), with higher responses at higher species richness (electronic supplementary material, figure S2). The correlations between the response magnitudes of ecosystem C pools and species richness also confirmed this result. We found the correlations between the response magnitude of aboveground biomass and species richness to be slightly different from that of belowground biomass (figure 5a,b). For aboveground biomass, our results confirmed earlier studies [72,75] showing an increase at low diversity, and then the relationship
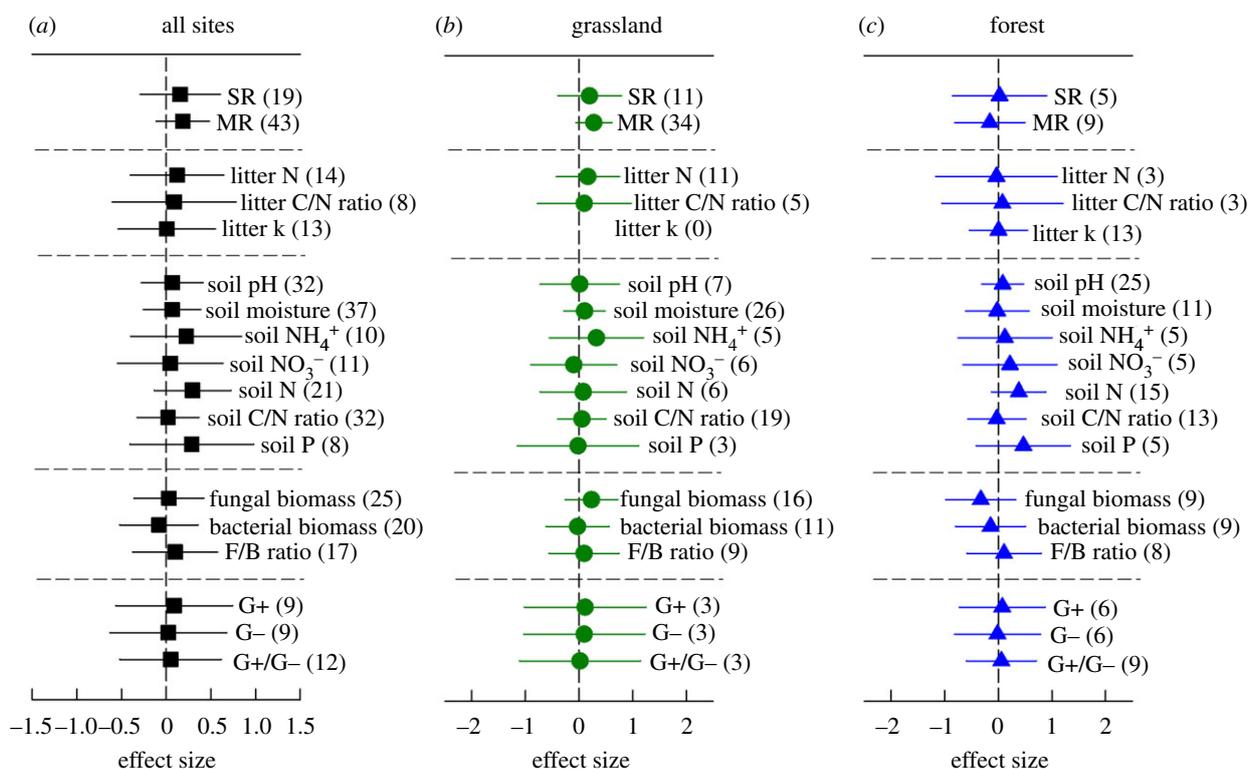
Figure 7. The effects of plant species richness on soil respiration, litter decomposition, soil physico-chemical properties and soil microbial communities (a) across all ecosystems, (b) in grassland and (c) in forest. SR, soil respiration; MR, microbial respiration; N, nitrogen; C/N, carbon to nitrogen ratio; litter k, litter decomposition rate; NH_4^+, ammonium; NO_3^-, nitrate; P, phosphorus; F/B, fungi to bacteria ratio; G+, Gram-positive bacterial biomass; G−, Gram-negative bacterial biomass; G+/G−, Gram-positive to Gram-negative bacterial biomass ratio. Effect sizes are shown as natural log-response ratios for n studies per response variable. Effects are significant when confidence intervals do not overlap with zero (indicated by asterisks, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$). Numbers in parentheses represent the number of observations for each parameter. (Online version in colour.)

decreased at high species richness (after 16 species). However, belowground biomass increased linearly with species richness both across all ecosystems and grassland (figure 5b). We need to mention that the species richness effect on belowground biomass could only be analysed for up to 16 species, whereas the species richness effect for aboveground biomass could be analysed up to a level of 60 species [76] (figure 5a, b). But the number of data points with more than 16 species is only two for aboveground biomass (figure 5a). When we log-transformed the species richness or deleted the two data points that >16 species, the patterns for the relationship of aboveground biomass and species richness changed, but still with an significantly increasing trend (electronic supplementary material, figure S3 and S4). Currently, we are unable to predict whether the response magnitude of belowground biomass will level off when the species richness level exceeds 16 species, although a related meta-analysis found that the responses of root biomass increased linearly with species richness up to 60 species [44]. However, we also found that the response magnitude of belowground biomass was significantly positively related to that of aboveground biomass (figure 4a). This result confirms the assumption that above- and belowground overyielding occur simultaneously in one plant community [19]. Notably, plant diversity effects on belowground biomass may need longer to materialize due to the accumulation of root biomass over time [77]. This may be particularly the case for forests.

Soil C content was also significantly increased with higher plant species richness (figure 3). These findings were consistent across grassland and forest (figure 3). We found that across all grassland studies the response magnitude of soil C content was significantly related to the response magnitude of aboveground biomass and belowground biomass (figure 4d,e). This suggests that plant species richness promoted soil C content by increasing plant C inputs and soil microbial activities (figure 1), which has been experimentally shown in several case studies in grassland [9,12,78]. For example, plant diversity was found to increase soil C storage by enhancing plant C inputs and stimulating soil microbial activities in a long-term grassland biodiversity experiment [12]. However, in our meta-analysis, belowground biomass in forest was not altered by higher plant species richness (figure 3). In addition, in forest, the response magnitude of soil C content had no significant correlation with that of aboveground biomass or belowground biomass (figure 4d,e). We suggest that apart from the quantity of plant C inputs, other factors affected the increase in soil C content with higher plant species richness in forest, such as the quality of plant inputs [36]. For example, by using structural equation models to analyse the inventory data across China's forests, plant diversity was shown to decrease litter C/N ratio and thus favour soil C accumulation [39]. Although our results showed litter C/N ratio was not altered with higher plant species richness across all ecosystems (figure 7), the data for litter C/N ratio were mainly from grassland, and we lack of data to test the potential effects of litter C/N ratio in forest. Therefore, more studies should focus on the mechanisms underlying the increase in soil C content with higher plant species richness in forest. But we also need to highlight that although a positive soil C content response to species richness suggests greater soil C storage, the soil C stock response remains incomplete without assessing potential changes in soil bulk density. This is because species richness could not

only affect soil C content, as shown here, but also bulk density, which could either increase or decrease the response of soil C storage. Therefore, we also suggest that further work on total soil C (that includes bulk density) will be needed to more comprehensively address species richness effects on the soil C pool.

(b) Ecological and experimental modulators of the effects of plant species richness on ecosystem C storage

The magnitude of the relationship between plant diversity and ecosystem C storage may be scale- and environment-dependent [27,64,79]. We thus used linear regressions and linear mixed-effects models to analyse how the ecological modulators (i.e. aridity index) and experimental modulators (i.e. plot area and experimental duration) affected the correlations between species richness and the response magnitudes of the four C pools.

Given that climate is known to be an important factor driving plant species richness, plant interactions, as well as C dynamics under natural conditions [4,80], we initially expected that the level of aridity, as indicated by the aridity index, will affect the responses of the four C pools to high plant diversity (i.e. BEF relationships are expected to decrease under more arid conditions; figure 1). However, the results from both linear mixed-effects models and linear regressions suggest that the aridity index did not significantly affect the responses of aboveground biomass, microbial biomass C and soil C content to plant diversity (table 1 and figure 6a,c,d). In addition, we also found that their responses were not correlated with MAT or MAP (electronic supplementary material, figure S5). However, the response magnitude of belowground biomass was increased with increasing aridity index and decreased with increasing MAP (figure 6b; electronic supplementary material, figure S5f). This was probably because sites with different aridity indices have different levels of soil moisture, and thus affect the responses of the belowground biomass to high plant diversity directly and indirectly through soil nutrient availability [81,82]. These results show limited impacts of climatic conditions on BEF relationships, which contradicts our hypothesis stating that biodiversity effects depend on environmental stress including drought [22,23]. Given that the aridity index and MAP ranged from 23.56 to 149.73 and from 492 mm to 4667 mm, respectively, in our dataset, these results call for studies across different and more extreme ecosystem types. In addition, the significant responses of belowground biomass indicate that these future studies should explore if aridity changes biodiversity effects on aboveground versus belowground biomass allocation, which could have subsequent cascading effects on other ecosystem processes.

Species richness and niche complementarity effects are suggested to be dominant predictors of ecosystem properties at small spatial scales, while environmental gradients explain variations in ecosystem properties at larger spatial scales [28,83]. This implies that the magnitude of the relationship between plant diversity and ecosystem C storage may be scale-dependent [28,29]. Our results from regression analysis suggested that the response magnitude of aboveground biomass decreased with increasing plot area in grassland, whereas the response magnitude of belowground biomass decreased with increasing plot area across ecosystems (figure 6e,f). These findings contradict the hypothesis that

biodiversity effects on plant biomass increase at larger spatial scales [26,28]. However, the reader should note that the plot area in our study ranged from less than 1 m² to 2500 m² distributed across multiple ecosystems. This means that, while these studies can test the underlying mechanisms of BEF and predictions of the theory within a limited spatial scale, they have limitations to address theoretical predictions that extend BEF relationships to larger spatial scales. However, the responses of microbial biomass C and soil C content had no significant correlations with plot area (figure 6g,h), suggesting that the responses of soil C content to species richness are not plot area-dependent. However, only few previous empirical studies have investigated how and why plot area affects the response of soil C content to plant species richness [84], and the proposed underlying mechanisms [28] need further research. The present results contradict with some of these theoretical considerations, which might be due to the fact that experimental plots typically are quite homogeneous, limiting different species and biodiversity facets to exert positive biodiversity effects at larger spatial scales. Moreover, the experimental plots studied here might still be too small and may not cover the environmental gradients considered [28].

Apart from the spatial effect on the plant diversity–ecosystem C storage relationship, the temporal trends of plant diversity effects on ecosystem C storage are also important for us to understand. Our results showed that the response magnitudes of the four C pools to high plant diversity increased with experimental duration (table 1 and figure 6i–l), which implies that the positive effect of plant diversity on ecosystem C storage may accumulate through time. The stronger effect of plant diversity on aboveground biomass over time in grassland and forest has also been reported by some BEF studies, and this was attributed to the changes in abiotic and biotic soil characteristics with experimental duration [42,85]. In our study, we also found that the response magnitudes of soil moisture and soil N content increased over time (data for up to 14 years; electronic supplementary material, figure S6), which can provide a favourable environment for plant growth. However, it has to be noted that in the dataset of our study, the experimental duration for aboveground biomass, belowground biomass and microbial biomass C was typically shorter than 25 years. As a consequence, there is still uncertainty whether the results stemming mostly from short-term experiments can reflect the responses of ecosystem C storage to plant species richness in the long term [3,72]. Data availability from long-term studies remains one of the main challenges for understanding the temporal trends of BEF relationships. We thus support the call to maintain existing experiments and to explore long-term BEF relationships [29,30].

In conclusion, in our study, we found that plant diversity promotes plant growth and C storage across C pools. Strong positive linkages among C pools suggest that enhanced plant biomass production increases soil microbial biomass and soil C storage across ecosystem types. Ecosystem C storage in grassland seems to be more responsive to plant species richness than in forest, pointing towards long-term dynamics in forest ecosystems. Notably, although our study provided strong empirical evidence for the significant positive role of plant diversity in ecosystem C storage across ecosystem types, climatic conditions and plot sizes, some of the findings might still be biased by the short-term duration of many BEF experiments (all less than or equal to 25 years). Moreover,

plant diversity effects on belowground plant biomass increased with increasing aridity index in grasslands and forests, suggesting that climate change might modulate biodiversity effects, with weaker effects under more arid conditions, and with potential implications for above and belowground biomass allocation. Since plant diversity effects on different C pools likely need many years to materialize, more long-term BEF studies are needed, especially so in forest ecosystems.

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