Environmental Research Letters

OPEN ACCESS

RECEIVED
24 January 2020

REVISED
6 August 2020

ACCEPTED FOR PUBLICATION
14 August 2020

PUBLISHED
1 October 2020

LETTER

Negative impacts of plant diversity loss on carbon sequestration exacerbate over time in grasslands

Chao Wang[1], Yujia Tang[2], Xiaona Li[1], Weiwei Zhang[1], Chunqiao Zhao[1] and Cui Li[1]

[1] Beijing Research and Development Center for Grasses and Environment, Beijing Academy of Agriculture and Forestry Sciences (BAAFS), No. 9 Shuguang Garden Middle Road, Haidian District, Beijing 100097, People's Republic of China

[2] School of Life Sciences, Capital Normal University, Beijing 100048, People's Republic of China

E-mail: 6521@cnu.edu.cn

Keywords: plant diversity, carbon attributes, experimental duration, complementary effects, grasslands

Supplementary material for this article is available online

Abstract

Positive relationships between plant species diversity and carbon attributes have been observed in grasslands, but synthesis studies of how plant diversity affects the carbon balance of grasslands and how the response ratio changes over time both remain limited. By conducting a global meta-analysis with 811 paired observations of plant mixtures and monocultures from 83 studies in natural and manipulated grasslands, we investigated the impacts of plant diversity on six carbon attributes, its interaction with experimental duration, and the changes in carbon balance under different plant diversity loss scenarios in the future. We found that the aboveground biomass (AGB), belowground biomass (BGB), total biomass (TB), soil organic carbon (SOC), soil respiration (Rs), and heterotrophic respiration (Rh) significantly increased in the plant mixtures, and the response ratio for all carbon attributes increased logarithmically with species richness. We also found that the response ratio for all carbon attributes except Rs increased linearly with experimental duration. The increase in response ratio of AGB, BGB, TB, and SOC with species richness was more pronounced with the long-term experimental duration. Importantly, our results showed that the declines in carbon sequestration will be exacerbated by different plant diversity loss scenarios in the future. Our meta-analysis revealed that plant diversity loss has ubiquitous negative impacts on multiple carbon attributes in grasslands, underlined the interactive effects of plant diversity loss and experimental duration on carbon attributes, and suggested that the reduction of carbon storage in grasslands following biodiversity loss will be greater in the future.

1. Introduction

Human activities, such as land use change and nitrogen deposition, lead to biodiversity loss at the global scale (Sala *et al* 2000, Gossner *et al* 2016, Harpole *et al* 2016, Wang and Tang 2019). a recent study showed that the world's seed-bearing plants have been disappearing at a rate of nearly three species a year since 1900, a rate up to 500 times higher than that which would be expected as a result of natural forces alone (Ledford 2019). One of the major advances in ecology over the last three decades is the demonstration that increased plant diversity has positive effects on a wide range of ecosystem functions, such as aboveground biomass (AGB) (Tilman *et al* 2001, Reich *et al* 2004, Prieto *et al* 2015), belowground biomass (BGB) (Mueller *et al* 2013, Ravenek *et al* 2014, Oram *et al* 2018), and soil organic carbon (SOC) (Fornara and Tilman 2008, Lange *et al* 2015, Yang *et al* 2019). Several recent meta-analyses have revealed that these ecosystem functions have been generally improved in plant mixtures at the global scale (Cardinale *et al* 2007, Zhang *et al* 2012, Ma and Chen 2016). Despite this, few studies have explored the relationship between plant diversity and multiple carbon attributes (Bardgett *et al* 2009, Hidy *et al* 2007, Piao *et al* 2009). Grasslands are one of the most widespread ecosystem types in the world and play a critical role in the global carbon cycle (Ni 2002, Suttie *et al* 2005, Kang *et al* 2007, Fang *et al* 2010). This lack of understanding of the effect of plant diversity on the carbon balance in grasslands has cast doubt on the predictability of terrestrial models (Abreu et al 2017).

Numerous studies have shown close relationships between plant diversity and carbon balance (including carbon inputs and outputs) in grasslands (Hector et al 2010, Craven et al 2016, Cowles et al 2016, Yang et al 2019). Plant diversity has been reported to have a positive effect on AGB—that is, 'overyielding' in plant mixtures compared with monocultures (Tilman et al 2001, Isbell et al 2009, Hector et al 2010, Craven et al 2016), and complementary effects have been proposed to explain this overyielding (Yachi and Loreau 1999, Loreau and Hector 2001, Cardinale et al 2007, Prieto et al 2015). Similarly, overyielding in BGB recently has been reported (Cowles et al 2016, Ma and Chen 2016). Several mechanisms have been proposed to explain this phenomenon, including diversity in belowground niches (complementary effects) (Dimitrakopoulos and Schmid 2004, Oram et al 2018), interspecific root interactions (de Kroon 2007, Mommer et al 2015), and lower pathogenic pressures (Brassard et al 2013, Mueller et al 2013) in plant mixtures. Neutral or negative effects caused by the plant diversity on AGB and BGB also have been reported (Malchair et al 2010, Ravenek et al 2014, Leloup et al 2017). Increased diversity had significant effects on plant biomass, followed by changes in SOC, soil respiration, and heterotrophic respiration (Rh) (Catovsky and Hector 2002, De Boeck et al 2007, Strassburg et al 2010, Abreu et al 2017, Chen et al 2019). It has been reported that SOC was higher in plant mixtures than monocultures because of increased AGB (Cong et al 2014) or BGB (Yang et al 2019), whereas other studies have shown that increased plant diversity had neutral or negative effects on SOC (Dijkstra et al 2005, Fornara and Tilman 2008, Malchair et al 2010). The decrease of soil respiration (Rs) following diversity loss was caused by the reduction in BGB or SOC (Craine et al 2001, De Boeck et al 2007), whereas the decline of Rh may be caused by reductions in litter production, SOC, and soil microbial biomass following diversity loss (Adair et al 2009, Malchair et al 2010, Chen et al 2019). Plant diversity loss causes a reduction in both carbon inputs and outputs simultaneously, and thus the source/-sink dynamics of grassland ecosystems remains controversial.

Temporal changes in the effects of plant diversity loss on carbon attributes have been previously reported in the studies and meta-analyses (Zhang et al 2012, Chen and Chen 2019, Chen et al 2019, 2020). Tilman et al (2001) first found that the effect of increased species on AGB became progressively stronger over time in grasslands. Potential reasons for the temporal changes in the effects of diversity loss on AGB include the decrease in complementarity effects over time (Cardinale et al 2007) or the decrease of functional redundancy over time (Reich et al 2012). Similarly, most recent meta-analyses have shown that the effects of diversity loss on BGB, SOC, and microbial respiration decreased linearly with experimental age in grasslands (Ma and Chen 2016, Chen and Chen 2019, Chen et al 2019, 2020). Because the negative effects of plant diversity loss on carbon inputs and outputs have occurred simultaneously, the carbon balance of grassland ecosystems following biodiversity loss remains controversial Therefore, improving our knowledge about these changes in multiple carbon attributes following plant diversity loss over time is crucial to predict carbon balance in grasslands under different biodiversity loss scenarios.

In this study, we compiled data from 83 studies to examine the effects of plant diversity loss on natural and manipulated grasslands, measured as the ratio of the main carbon inputs (AGB, BGB and TB), outputs (Rs and Rh), and balance (SOC) in plant mixtures to the average of those in monocultures. We specifically tested whether: (1) plant mixtures showed a greater carbon sink than monocultures in grasslands; (2) the positive effects of plant diversity on six carbon attributes increased with experimental duration; and (3) the reduction in carbon sequestration of grassland ecosystems following plant diversity loss would be exacerbated over time.

2. Material and methods

2.1. Data collection

We searched all peer-reviewed publications that investigated the effects of plant diversity on carbon pools and fluxes in grasslands using the ISI Web of Science (isiknowledge.com), Google Scholar (www.scholar.google.com), and the China National Knowledge Infrastructure (CNKI, www.cnki.net) through December 31, 2019. We used different keyword combinations, including grassland, biomass, production/productivity, aboveground, belowground, root, SOC, Rs, Rh, carbon pool, carbon flux, diversity, mixtures, pure, monoculture, and richness were used for the search. We applied the following criteria to select the appropriate observations: (1) experiments had at least one pair of data at the same temporal and spatial scales (under monoculture and mixtures), including carbon pools and fluxes; (2) the effect of diversity was clearly described, including diversity level (species richness) and experimental duration; and (3) the means, standard deviations/errors and samples size of variables in the monoculture and mixtures groups could be extracted directly from the context, tables, or digitized graphs. In total, we selected 83 published papers and 811 observations about the effects of diversity on carbon pools and fluxes (Wang et al 2020), of which there were 34 on AGB, 17 on BGB, 4 on TB, 11 on SOC, 8 on Rs, and 9 on Rh. A list of data sources and data is shown in table S1 and S2 in the supplementary information (available online at http://stacks.iop.org/ERL/15/104055/mmedia).

For each study, we extracted the data on AGB, BGB, TB, SOC, Rs, Rh, complementary effects (CE), selection effects (SE), species richness (SR), experimental duration (ED), and experimental types (ET, natural or manipulated) from the original papers. We derived the sample size corresponding to each observation based on the number of independent experimental units. All the data were obtained either from tables or extracted from figures using the GetData Graph Digitizer (ver. 2.24, <www.getdata-graph-digitizer.com/>). In addition, we divided the experimental duration into three groups: 1 (1–3 years), 4 (4–8 years), and 8 (>8 years).

2.2. Data analysis

We followed the methods used by Hedges *et al* (1999) and Gurevitch *et al* (2018) to evaluate the effects of diversity on carbon attributes. A metric commonly used in meta-analysis, response ratio (*lnRR*, natural log of the ratio of the mean value of monoculture plots to that in mixtures) was calculated as below:

$$lnRR = \ln\left(\frac{\bar{x}_t}{\bar{x}_c}\right) = \ln(\bar{x}_t) - ln(\bar{x}_c) \tag{1}$$

where x_t and x_c are means of the concerned variable in mixtures and monocultures, respectively. We used random effects models to analyze the weighted average RR and meta-regression in the study and estimated the between-sampling variability by the *rma* function based on restricted maximum likelihood estimation (*REML*) in R 3.5.1 (Chen and Peace 2013). Because estimates of effect size and subsequent inferences in meta-analysis may depend on how individual studies are weighted (van Groenigen *et al* 2011, Mueller *et al* 2012), we estimated the weights for studies by sampling standard deviations (standard deviations equal to standard errors multiplied by the square root of the sample size) (Hedges *et al* 1999) and the between-sampling variability (equation (2)):

$$w_v = \left(\frac{s_t^2}{n_t\bar{x}_t^2} + \frac{s_c^2}{n_c\bar{x}_c^2} + \tau^2\right)^{-1} \tag{2}$$

where S_t, n_t, S_c, and n_c are the standard deviation and sample size for the plant mixtures and monocultures, respectively, and τ^2 is total amount of heterogeneity.

For each carbon attribute, we tested whether *lnRR* was affected by plant diversity (PD), ED, and ET using the following model:

$$\begin{aligned} \ln RR = {} & \beta_0 + \beta_1 \times PD + \beta_2 \times ED + \beta_3 \times ET \\ & + \beta_4 \times PD \times ED + \beta_5 \times PD \times ET \\ & + \beta_6 \times ED \times ET + \beta_7 \times PD \\ & \times ED \times ET + \pi_{study} + \varepsilon \end{aligned} \tag{3}$$

where β is the coefficient to be estimated; π_{study} is accounting for the autocorrelation among observations within each study; and ε is sampling error. All the independent variables were standardized before fitting this model. We conducted the analysis using the *REML* with the *lme4* package with w_v as the weight for each corresponding observation (Bates *et al* 2015). To prevent overfitting (Johnson and Omland 2004), we selected the most parsimonious model among all alternatives as long as PD and ED were retained, because they were part of our core hypotheses to be tested (table S3).

We used random-effects meta-regression to evaluate the relationships among the response ratio of carbon attributes, plant diversity, and experimental duration. Plant diversity and experimental duration were the fixed effects, studies was the random effects, and w_v was the weight. We also used random-effects meta-regression to analyze the relationship between the complementary and selection effects of AGB and BGB and species richness (tables S5 and S6). Analysis of covariance was used to test whether the slopes for the relationship between plant diversity and response ratio differed significantly with varying experimental duration (tables S3 and S4). For ease of interpretation, we transformed *lnRR* and its corresponding 95% confidence intervals (CIs) to a percentage change between monocultures and mixtures as ($e^{lnRR}-1$) × 100%.

To illustrate the effects of plant diversity loss on carbon attributes over time, we compared the *lnRR* when the plant diversity in mixtures was R_1 (all species present) and R_α (α % lower species richness) using the following equation (Chen *et al* 2019):

$$P_\alpha = (R_1/R_\alpha)^{\beta_1+\beta_4 T} \tag{4}$$

where P_α is the proportion of remaining carbon attributes under α % lower plant species richness in a period of *T*, and other model terms were described in equation (3). Based on equation (4), we fitted curves for the decrease in carbon attributes over time when there was a 10%, 20%, 40%, and 80% decrease in species richness. We limited the forecasting to 30 years because that is the age of the longest field biodiversity experiment at Cedar Creek Natural History Area, Minnesota, USA (Tilman *et al* 2006).

We analyzed all data using R 3.5.1 and considered the statistical results to be statistically significant at $P \leq 0.05$. The graphs were drawn with the ggplot2 package in R 3.5.1 (R Core Team 2018).

3. Results

3.1. Average effects of plant mixtures on carbon attributes

Across all studies, the average effects of plant mixtures on carbon input attributes were larger than carbon outputs. AGB increased significantly by an average of 63.6% (95% confidence interval,

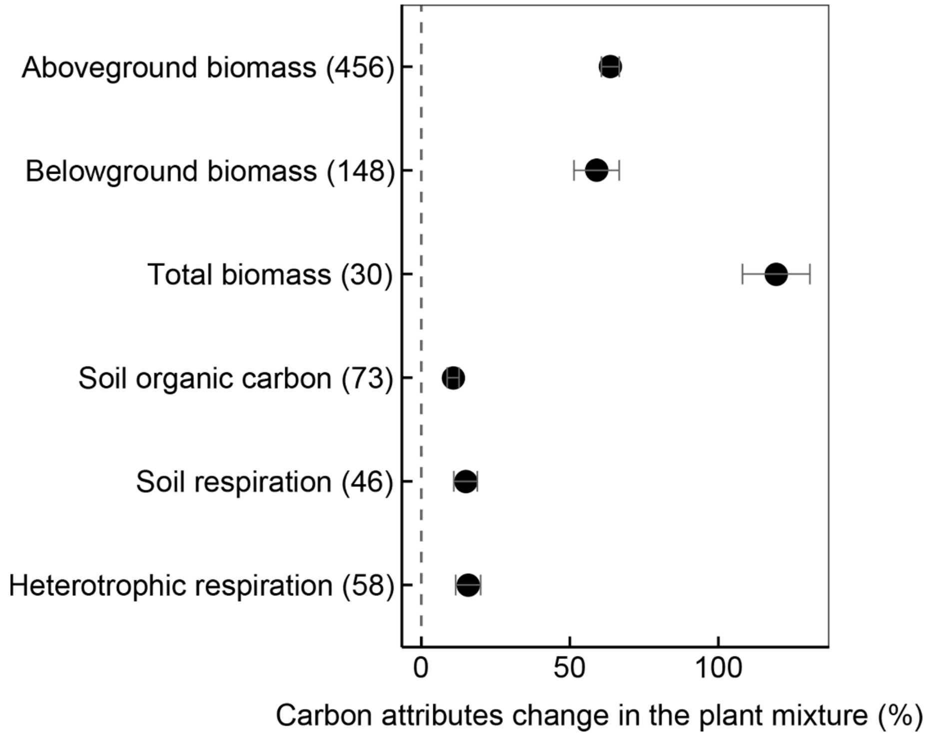

Figure 1. Comparison of carbon attributes between plant mixtures and monocultures in grasslands. The changes represent the increase or decrease (%) of a given carbon attribute compared to the corresponding mean of monocultures at the mean plant diversity and experimental duration in mixtures (see Methods). Values are mean ±95% confidence intervals of the percentage changes between the plant mixtures and monocultures. The number of observations for each attribute is displayed in parentheses.

58.9%–68.6%, figure 1), BGB by 59% (95% confidence interval, 47.8%–71.1%, figure 1), TB by 119.5% (95% confidence interval, 97.1%–144.3%, figure 1), SOC by 10.7% (95% confidence interval, 8.56%–12.9%, figure 1), Rs by 14.9% (95% confidence interval, 10.5%–19.5%, figure 1), and Rh by 15.8% (95% confidence interval, 11.1%–20.1%, figure 1) in plant mixtures compared with the average of those in monocultures.

3.2. The varying effects of plant mixtures

With increasing species richness in plant mixtures, the response ratio of AGB, BGB, TB, SOC, Rs, and Rh significantly increased (figure 2(a)). The response ratio of AGB ($P < 0.001$, table S4), BGB ($P < 0.001$, table S4), TB ($P = 0.004$, table S4), SOC ($P < 0.001$, table S4), and Rh ($P < 0.001$, table S5) increased linearly with experimental duration (figures 2(b) and 4), and the response ratio of Rs ($P = 0.99$, table S3) decreased (figures 2(b) and 4). The plant mixtures effect on carbon attributes did not differ significantly among experimental types including both natural and manipulated grasslands (figure 2(c)).

The effects of plant mixtures on carbon attributes differed with varying experimental duration (figure 3 and table S5). The increase of AGB ($P = 0.02$, tables S5 and S7), BGB ($P = 0.02$, tables S5 and S7), TB ($P = 0.10$, tables S5 and S7), and SOC ($P = 0.03$, tables S5 and S7) with species richness became more pronounced given longer experimental duration, whereas no effect was observed in Rs and Rh (tables S5 and S7).

3.3. Predicted responses of carbon attributes

Predicted from the fitted species richness- and experimental duration dependent responses (figure 5), a 10% decrease in plant diversity (from 100% to 90%) over one year reduced AGB, BGB, TB, SOC, Rs, and Rh by 0.82%, 1.62%, 1.11%, 0.68%, 0.16%, and 0.28%, respectively (figure 5(a)). A 40% decrease in plant diversity (from 100% to 60%) over one year led to 3.74%, 7.14%, 4.80%, 3.21%, 0.76%, and 1.32% reductions in AGB, BGB, TB, SOC, Rs, and Rh, respectively (figure 5(c)). The declines in carbon attributes in response to the decrease in plant diversity were amplified by longer experimental duration, whereas the amplification for carbon input attributes was larger than for carbon outputs (figure 5). For example, a 10% decrease in plant diversity (from 100% to 90%) over five years led to 4.01% and 7.82% reductions in AGB and BGB, respectively, but led to 0.79% and 1.39% declines in Rs and Rh, respectively (figure 5(a)).

4. Discussion

Many studies have explored the response of carbon attributes to plant diversity. Three aspects of our study, however, distinguish it from these previous studies. First, although a few studies of have

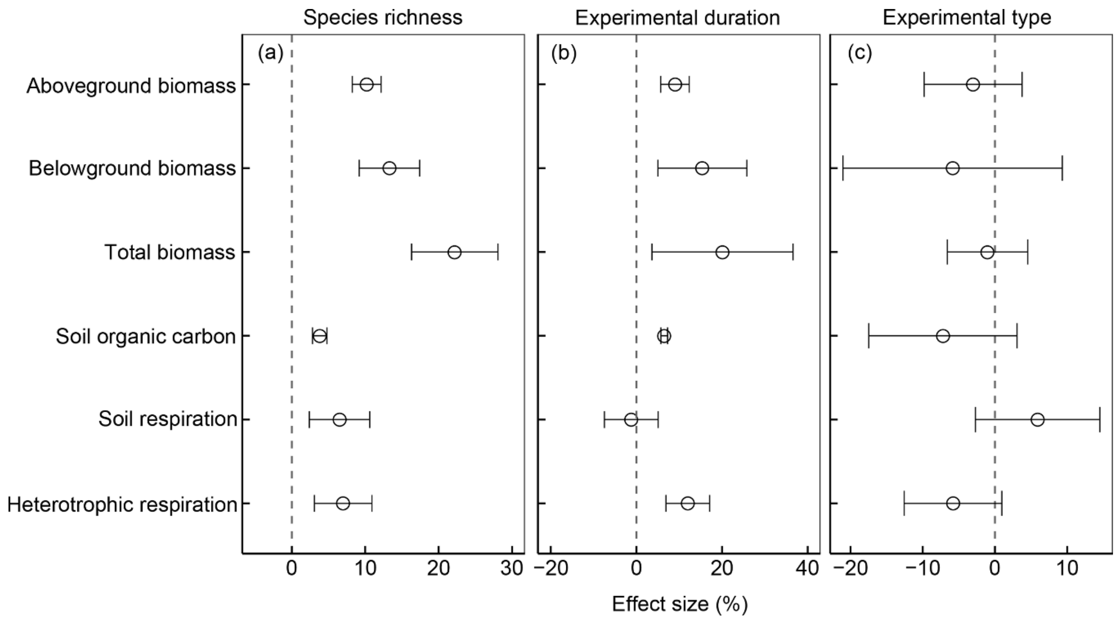

Figure 2. The effects of plant mixtures on carbon attributes in relation to species richness, experimental duration, and experimental duration (natural or manipulated) in grasslands. The species richness (log scale) in plant mixtures (a), experimental duration (years) (b), and experimental types (c). The effects represent the estimated coefficients of the species richness in mixtures, experimental duration, and experimental types. Values (estimated β_1, β_2, and β_3 in equation (3), respectively) are mean ±95% confidence intervals.

considered the effects of plant diversity on single carbon attributes, our study examined the response of six carbon attributes in a meta-analysis. Second, our study explored the interactive effects of plant diversity loss and experimental duration on six carbon attributes. Third, and most important, through prediction models, we confirmed that the declines in carbon balance in response to plant diversity loss became amplified over time in grasslands.

4.1. Carbon sink increased in plant mixtures

We found evidence to generally support the hypothesis that plant mixtures showed a greater carbon sink than monocultures in grasslands. Two aspects of our study confirmed this hypothesis. First, soil organic carbon, which is the net balance of carbon in ecosystems, significantly increased in the plant mixtures. Second, net carbon balance also could be estimated by the primary production and Rh. Larger increases in AGB and BGB than Rh in plant mixtures led to an increase in carbon sink. Specifically, AGB and its complementary effects increased logarithmically with species richness in grasslands. These findings were consistent with the results of a meta-analysis by Cardinale *et al* (2007), in which the increase in AGB was attributable to the amplification of niche complementarity with species richness (figure S3(a)). As with AGB, the increase in BGB was caused by the increase of complementary effects belowground (figure S3(c)), which was consistent with results in forests obtained by Ma and Chen (2016). TB is the combination of AGB and BGB, and the increase in complementary effects of AGB and BGB induced the increase of TB in plant mixtures (Cowles *et al* 2016).

Similar to the results for plant systems, SOC, Rs, and Rh also increased logarithmically with species richness. We attributed the increase in SOC to the increase of BGB with species richness (figure S4(b)). It has been reported that increased in SOC and BGB were followed by an increase in soil carbon resources (Craine *et al* 2001, Chen *et al* 2019), which has resulted in an increase of Rh in plant mixtures. Rs is the combination of Rh and root respiration (Wang *et al* 2017). Increases in BGB strengthen root respiration (Luo and Zhou 2006), and thus increases in both Rh and root respiration caused the rise in Rs in plant mixtures.

4.2. The effect sizes changed with experimental duration

Numerous studies have shown that the effects of plant diversity on ecosystem functions increase with experimental duration or stand age (Tilman *et al* 2001, Chen *et al* 2019, 2020). The increase in the response ratios of AGB and BGB with experimental duration was consistent with the results of Tilman *et al* (2001) and Ravenek *et al* (2014), which may be attributable to the increased magnitude of complementarity over time (Cardinale *et al* 2007). The response ratio of TB increased with experimental duration, which may be due to the increased magnitude of niche complementarity over time both above- and below ground. We found that the increase in the response ratio of SOC with experimental duration was caused by an increased response ratio in BGB, and the increase in

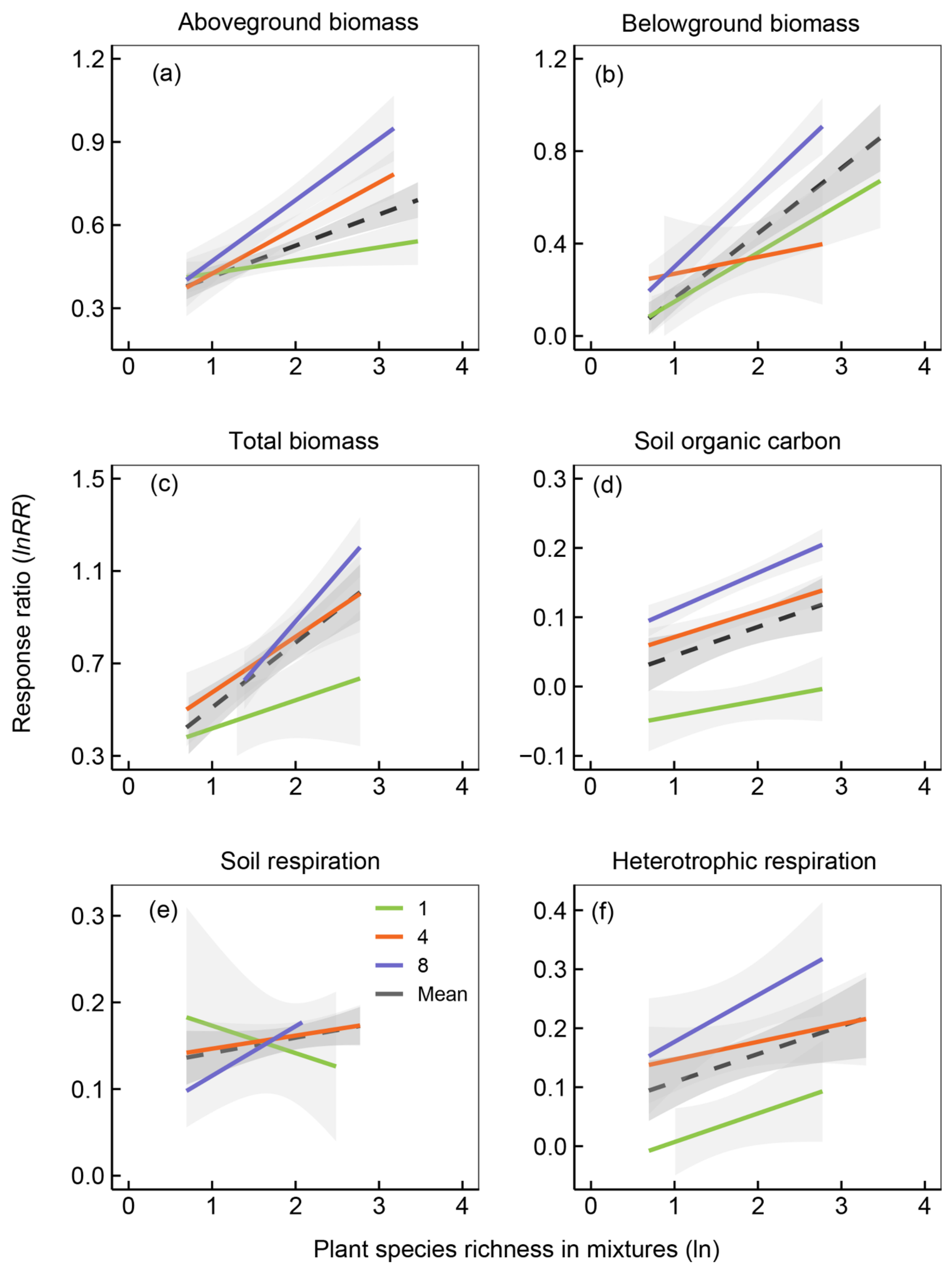

Figure 3. The interactive effects of species richness in plant mixtures and experimental duration on carbon attributes in grasslands. Plots show the aboveground biomass (a), belowground biomass (b), total biomass (c), soil organic carbon (d), soil respiration (e), and heterotrophic respiration (f) in relation to species richness from random effects meta-regression. Green, orange, purple and grey lines indicate experimental duration at 1, 4 and 8 years and experimental duration across all observations, respectively. Shaded areas show 95% confidence interval of the fit. RR, response ratio.

the response ratio of Rh over time was caused by the increase in SOC.

Our results revealed the interactive effects of plant diversity and experimental duration on carbon inputs and balance in grasslands, but not for carbon outputs. These results did not support our second hypothesis that the negative effects of plant diversity loss on carbon attributes were amplified with experimental duration. Given the positive relationship between the response ratio of AGB and BGB and complementary effects (figure S2), the enhancement of complementary effects with increased species richness (figure S3) and extended experimental duration (Cardinale *et al* 2007, Ravenek *et al* 2014) led to an enhancement in

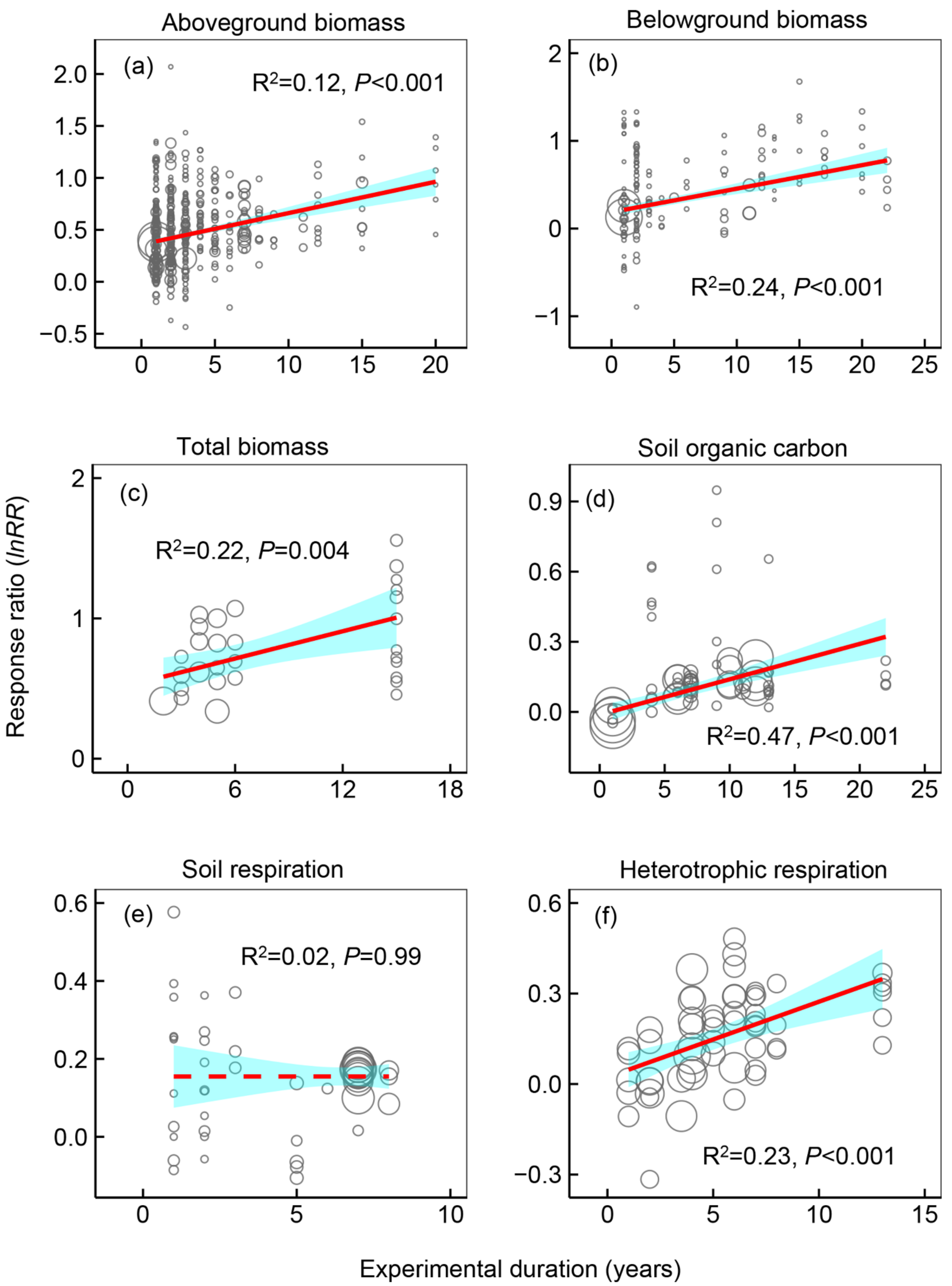

Figure 4. The relationship between experimental duration and the response ratios (RR) for carbon attributes in grasslands. Plots show the natural log response ratio (*lnRR*) of aboveground biomass (a), belowground biomass (b), total biomass (c), soil organic carbon (d), soil respiration (e), and heterotrophic respiration (f) in relation to species richness from random effect meta-regression. The sizes of the circles represent the relative weights of corresponding variance. Solid lines represent significant relationships ($P < 0.05$), dashed lines represent insignificant, shaded areas show 95% confidence interval of the fit.

the response ratio of AGB and BGB over time. TB is the combination of AGB and BGB, the combined effects of plant diversity and experimental duration on TB were caused by their combined effects on AGB and BGB. Moreover, we found that the amplification of the response ratio of SOC was induced by changes in BGB (figure S4(b)), and thus higher carbon inputs belowground led to greater carbon storage in the soil (Yang *et al* 2019).

The response ratio of carbon outputs over time, however, differed from carbon inputs. There were no interactive effects of plant diversity and experimental

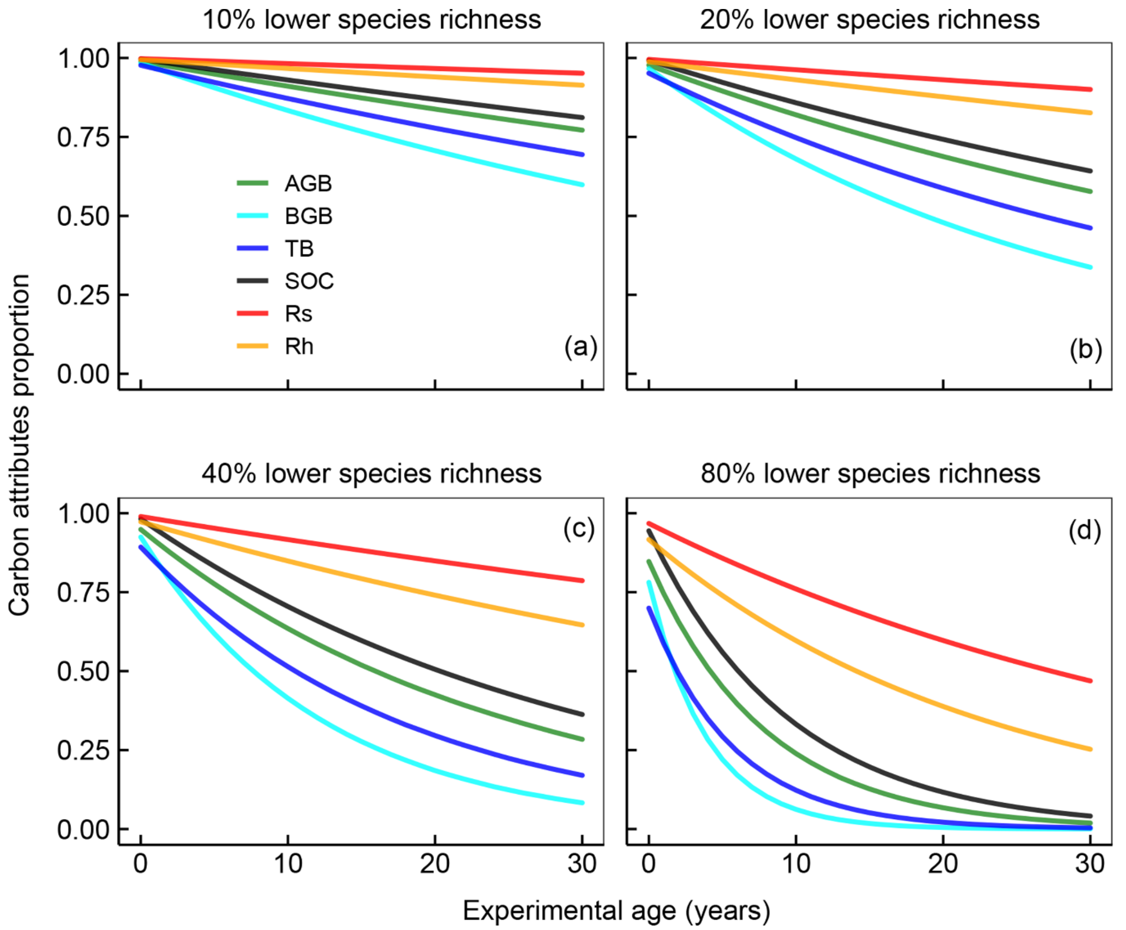

Figure 5. Predicted responses of carbon attributes to a range of plant species richness reductions in grasslands. Plots show the plant species richness reduction at 10% (a), 20% (b), 40% (c) and 80% (d). Lines with different colors represent different carbon attributes. AGB, aboveground biomass; BGB, belowground biomass; TB, total biomass; SOC, soil organic carbon; Rs, soil respiration; Rh, heterotrophic respiration.

duration on Rs and Rh, which was inconsistent with the results of meta-analyses by Chen and Chen (2019) and Chen *et al* (2019) across all terrestrial ecosystems. Plant diversity increased Rh by increasing SOC (figure S4(c)), whereas the accelerative increase in SOC over time led to an increase in carbon to nitrogen ratios in the soil and root systems (Prommer *et al* 2019). We did not observe the subsequent decrease in substrate quality (high carbon-to-nitrogen ratio) for microbes to cause significant changes in the response ratio of Rh over time. Our previous studies found that Rh accounted for more than half of the total Rs (Ren *et al* 2016, Wang *et al* 2017), and thus the trends in the response ratio of Rh over time determined the changes in Rs. Most of the studies for Rs and Rh in grasslands were eight years or less in duration, and thus the short duration of studies that have measured Rs and Rh did not reveal significant interactive effects of plant diversity and experimental duration.

4.3. Carbon sequestration under plant diversity loss over time

We found evidence to support our third hypothesis that decreases in carbon sink under plant diversity loss in grasslands were enhanced with experimental duration. Our results showed that a 10% (from 100% to 90%) decrease in plant species richness caused a small decline in SOC over one year, but a larger cumulative decline over five years in grasslands. Our results also showed that a 10% (from 100% to 90%) decrease in species richness caused a reduction of only 0.28% in Rh, while leading to declines of 0.82% and 1.62% in AGB and BGB, respectively. Thus, the faster decrease in carbon inputs versus outputs with extended experimental duration led to accelerated reduction in carbon storage in grasslands following plant diversity loss. As the diversity of plant communities worldwide declines under global warming (Tilman and Lehman 2001, Tylianakis *et al* 2008), the rising negative effects of plant diversity loss on carbon storage over time may enhance the positive feedback of greenhouse effects, further accelerating global warming. Moreover, as plant species richness in communities fluctuates over time, ecosystems will adapt to the environmental changes after a certain period (Bezabih and Geback 2010), and thus our prediction model, which was based on a fixed decrease rate over time, may have overestimated the reduction in the carbon balance of grasslands.

5. Conclusions

Our meta-analysis provided comprehensive evidence that greater plant diversity can have a positive effect on carbon input (aboveground and belowground biomass, total biomass), output (soil respiration and heterotrophic respiration), and carbon balance (soil organic carbon) attributes in grasslands, but the increase in carbon inputs was larger than the increase in outputs. These results suggested that carbon sink in the plant mixtures was larger than monocultures. Our study determined that the effects of plant diversity on carbon attributes were enhanced with experimental duration, except for soil respiration. This demonstrated that plant mixtures develop a faster carbon turnover rate over time. Furthermore, our study predicted that the amplification for declines in carbon input attributes over time was larger than the declines in outputs in response to the decrease in plant diversity.

Acknowledgments

This study was supported by National Natural Science Foundation of China (Grant No. 31 901 173), Beijing Natural Science Foundation (Grant No. 5 204 030), and Beijing Academy of Agriculture and Forestry Sciences (BAAFS) Special Project on Hi-Tech Innovation Capacity (Grant No. KJCX20200431 and KJCX20180707). We would like to acknowledge the work carried out by the researchers whose published data was used in this meta-analysis.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://figshare.com/s/d010fecd1d9987a2231a.

ORCID iD

Chao Wang https://orcid.org/0000-0002-8916-4735

References

Abreu R C R, Hoffmann W A, Vasconcelos H L, Pilon N A, Rossatto D R and Durigan G 2017 The biodiversity cost of carbon sequestration in tropical savanna *Sci. Adv.* **3** e1701284

Adair E C, Reich P B, Hobbie S E and Knops J M 2009 Interactive effects of time, CO_2, N and diversity on total belowground carbon allocation and ecosystem carbon storage in a grassland community *Ecosystems* **12** 1037–52

Bardgett R D, De Deyn G B and Ostle N J 2009 Plant-soil interactions and the carbon cycle *J. Ecol.* **97** 838–912

Bates D, Mächler M, Bolker B and Walker S 2015 Fitting linear mixed-effects models using lme4 *J. Stat. Software* **67** 1–48

Bezabih M and Geback T 2010 Environmental change and the contribution of biodiversity to ecosystem adaptation *Nat. Resour. Model.* **23** 253–84

Brassard B W, Chen H Y H, Cavard X, Laganière J, Reich P B, Bergeron Y, Paré D and Yuan Z 2013 Tree species diversity increases fine root productivity through increased soil volume filling *J. Ecol.* **101** 210–9

Cardinale B J, Wright J P, Cadotte M W, Carroll I T, Hector A, Srivastava D S, Loreau M and Weis J J 2007 Impacts of plant diversity on biomass production increase through time because of species complementarity *Proc. Natl Acad. Sci. USA* **104** 18123–8

Catovsky S and Hector B A 2002 Biodiversity and ecosystem productivity implications for carbon storage *Oikos* **97** 448–58

Chen C, Chen H Y H, Chen X and Huang Z 2019 Meta-analysis shows positive effects of plant diversity on microbial biomass and respiration *Nat. Commu.* **10** 1332

Chen D-G and Peace K E 2013 Chapman & Hall/CRC Biostatistics Series *Applied meta-analysis with R* (Boca Raton, FL: CRC Press)

Chen X and Chen H Y H 2019 Plant diversity loss reduces soil respiration across terrestrial ecosystems *Glob. Change Biol.* **25** 1482–92

Chen X, Chen H, Chen C, Ma Z, Searle E B, Yu Z and Huang Z 2020 Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis *Biol. Rev.* **95** 167–83

Cong W, van Ruijven J, Mommer L, De Deyn G B, Berendse F, Hoffland E and Lavorel S 2014 Plant species richness promotes soil carbon and nitrogen stocks in grasslands without legumes *J. Ecol.* **102** 1163–70

R Core Team 2018 *R: A Language and Environment for Statistical Computing* (Vienna: R Foundation for Statistical Computing)

Cowles J M, Wragg P D, Wright A J, Powers J S and Tilman D 2016 Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity *Glob. Change Biol.* **22** 741–9

Craine J M, Wedin D A and Reich P B 2001 The response of soil CO_2 flux to changes in atmospheric CO_2, nitrogen supply and plant diversity *Glob. Change Biol.* **7** 947–53

Craven D *et al* 2016 Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought *Phil. Trans. R. Soc. B* **371** 1–8

De Boeck H J, Lemmens C M H M, Vicca S, Van den Berge J, Van Dongen S, Janssens I A, Ceulemans R and Nijs I 2007 How do climate warming and species richness affect CO_2 fluxes in experimental grasslands? *New Phytol.* **175** 512–22

de Kroon H 2007 Ecology-how do roots interact? *Science* **318** 1562–3

Dijkstra F A, Hobbie S E, Reich P B and Knops J M H 2005 Divergent effects of elevated co2, n fertilization, and plant diversity on soil c and n dynamics in a grassland field experiment *Plant Soil* **272** 41–52

Dimitrakopoulos P G and Schmid B 2004 Biodiversity effects increase linearly with biotope space *Ecol. Lett.* **7** 574–83

Fang J, Yang Y, Ma W, Mohammat A and Shen H 2010 Ecosystem carbon stocks and their changes in China's grasslands *Sci. China Life Sci.* **53** 757–65

Fornara D A and Tilman D 2008 Plant functional composition influences rates of soil carbon and nitrogen accumulation *J. Ecol.* **96** 314–22

Gossner M M *et al* 2016 Land-use intensification causes multitrophic homogenization of grassland communities *Nature* **540** 266

Gurevitch J, Koricheva J, Nakagawa S and Stewart G 2018 Meta-analysis and the science of research synthesis *Nature* **555** 175–82

Harpole W S *et al* 2016 Addition of multiple limiting resources reduces grassland diversity *Nature* **537** 93

Hector A, Hautier Y, Saner P, Wacker L, Bagchi R, Joshi J and Caldeira M C 2010 General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding *Ecology.* **91** 2213–20

Hedges L, Gurevitch J and Curtis P 1999 The meta-analysis of response ratios in experimental ecology *Ecology.* **80** 1150–6

Hidy D, Barcza Z, Haszpra L, Churkina G and Trusilova K 2007 Parameter estimation for grassland carbon cycle using

nonlinear inversion of Biome-BGC *Cereal Res. Commun.* **35** 453–6
Isbell F, Polley H W and Wilsey B J 2009 Biodiversity, productivity and the temporal stability of productivity: patterns and processes *Ecol. Lett.* **12** 443–51
Johnson J B and Omland K S 2004 Model selection in ecology and evolution *Trends Ecol. Evol.* **19** 101–8
Kang L, Han X, Zhang Z and Sun O 2007 Grassland ecosystems in China: review of current knowledge and research advancement *Phil. Trans. R. Soc.* **362** 997–1008
Lange M *et al* 2015 Plant diversity increases soil microbial activity and soil carbon storage *Nat. Commun.* **6** 6707
Ledford H 2019 Global plant extinctions mapped *Nature* **570** 148–9
Leloup J, Baude M, Nunan N, Meriguet J, Dajoz I, Le Roux X and Raynaud X 2017 Unravelling the effects of plant species diversity and aboveground litter input on soil bacterial communities *Geoderma* **317** 1–7
Loreau M and Hector A 2001 Partitioning selection and complementarity in biodiversity experiments *Nature* **412** 72–76
Luo Y and Zhou X (Eds) 2006 *Soil Respiration and the Environment* (Amsterdam: Elsevier)
Ma Z and Chen H Y H 2016 Effects of species diversity on fine root productivity in diverse ecosystems: a global meta-analysis *Global Ecol. Biogeogr.* **25** 1387–96
Malchair S, De Boeck H J, Lemmens C M H, Merckx R, Nijs I, Ceulemans R and Carnol M 2010 Do climate warming and plant species richness affect potential nitrification, basal respiration and ammonia-oxidizing bacteria in experimental grasslands? *Soil Biol. Biochem.* **42** 1944–51
Mommer L, Padilla F M, van Ruijven J, de Caluwe H, Smit-Tiekstra A, Berendse F and Kroon H 2015 Diversity effects on root length production and loss in an experimental grassland community *Funct. Ecol.* **29** 1560–8
Mueller K E, Hobbie S E, Oleksyn J, Reich P B and Eissenstat D M 2012 Do evergreen and deciduous trees have different effects on net N mineralization in soil? *Ecology* **93** 1463–72
Mueller K E, Hobbie S E, Tilman D and Reich P B 2013 Effects of plant diversity, N fertilization, and elevated carbon dioxide on grassland soil N cycling in a long-term experiment *Glob. Change Biol.* **19** 1249–61
Ni J 2002 Carbon storage in grasslands of China *J. Arid Environ.* **50** 205–18
Oram N J *et al* 2018 Below-ground complementarity effects in a grassland biodiversity experiment are related to deep-rooting species *J. Ecol.* **106** 265–77
Piao S, Fang J, Ciais P, Peylin P, Huang Y, Sitch S and Wang T 2009 The carbon balance of terrestrial ecosystems in China *Nature* **458** 1009–13
Prieto I, Violle C, Barre P, Durand J L, Ghesquiere M and Litrico I 2015 Complementary effects of species and genetic diversity on productivity and stability of sown grasslands *Nature Plants* **1** 1–6
Prommer J, Walker T W N, Wanek W, Braun J and Richter A 2019 Increased microbial growth, biomass and turnover drive soil organic carbon accumulation at higher plant diversity *Glob. Change Biol.* **26** 669–81
Ravenek J M *et al* 2014 Long-term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time *Oikos* **123** 1528–36
Reich P B, Tilman D, Isbell F, Mueller K, Hobbie S E, Flynn D F B and Eisenhauer N 2012 Impacts of biodiversity loss escalate through time as redundancy fades *Science* **336** 589–92
Reich P B, Tilman D, Naeem S, Ellsworth D S, Knops J, Craine J, Wedin D and Trost J 2004 Species and functional group diversity independently influence biomass accumulation and its response to CO_2 and N *Proc. Natl Acad. Sci. USA* **101** 10101–6
Ren F *et al* 2016 Phosphorus does not alleviate the negative effect of nitrogen enrichment on legume performance in an alpine grassland *J. Plant Ecol.* **1** 1–9
Reynolds S and Batello C (eds) 2005 Grasslands of the World (Rome: Food and Agriculture Organization)
Sala O E *et al* 2000 Global biodiversity scenarios for the Year 2100 *Science* **287** 1770–4
Strassburg B B N *et al* 2010 Global congruence of carbon storage and biodiversity in terrestrial ecosystems *Conserv. Lett.* **3** 98–105
Tilman D and Lehman C 2001 Human-caused environmental change: impacts on plant diversity and evolution *Proc. Natl Acad. Sci. USA* **98** 5433–40
Tilman D, Reich P B and Knops J M H 2006 Biodiversity and ecosystem stability in a decade-long grassland experiment *Nature* **7093** 629–32
Tilman D, Reich P B, Knops J M H, Wedin D, Mielke T and Lehman C 2001 Diversity and productivity in a long-term grassland experiment *Science* **294** 843–5
Tylianakis J M, Didham R K, Bascompte J and Wardle D A 2008 Global change and species interactions in terrestrial ecosystems *Ecol. Lett.* **11** 1351–63
Wang C *et al* 2017 Soil respiration is driven by fine root biomass along a forest chronosequence in subtropical china *J. Plant Ecol.* **1** 36-46
Wang C and Tang Y 2019 A global meta-analyses of the response of multitaxa diversity to grazing intensity in grasslands *Environ. Res. Lett.* **14** 114003
Wang C, Tang Y, Li X, Zhang W, Zhao C and Li C 2020 Negative impacts of plant diversity loss on carbon sequestration exacerbate over time in grasslands *Environ. Res. Lett.* (https://doi.org/10.1088/1748-9326/abaf88)
Yachi S and Loreau M 1999 Biodiversity and ecosystem productivity in a fluctuating environment *Proc. Natl Acad. Sci. USA* **96** 1463–8
Yang Y, Tilman D, Furey G and Lehman C 2019 Soil carbon sequestration accelerated by restoration of grassland biodiversity *Nat. Commun.* **10** 718
Zhang Y, Chen H Y H and Reich P B 2012 Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis *J. Ecol.* **100** 742–9
van Groenigen K J, Osenberg C W and Hungate B A 2011 Increased soil emissions of potent greenhouse gases under increased atmospheric CO_2 *Nature* **475** 214–6