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

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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, Sutte et al 2005, Kang et al 2007, Fang et al 2010). This lack of under-
standing 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:

\[ \ln RR = \ln \left( \frac{\bar{x}_c}{\bar{x}_m} \right) = \ln (\bar{x}_c) - \ln (\bar{x}_m) \]  

where \( x_c \) and \( x_m \) 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 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)):

\[ w_i = \left( \frac{s_i^2}{n_i x_i^2} + \frac{s_c^2}{n_c x_c^2} + \tau^2 \right)^{-1} \]  

where \( s_i \), \( n_i \), \( s_c \), and \( n_c \) are the standard deviation and sample size for the plant mixtures and monocultures, respectively, and \( \tau^2 \) 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:

\[ \ln RR = \beta_0 + \beta_1 \times PD + \beta_2 \times ED + \beta_3 \times ET + \beta_4 \times PD \times ED + \beta_5 \times PD \times ET + \beta_6 \times ED \times ET + \pi_{study} + \varepsilon \]  

where \( \beta \) is the coefficient to be estimated; \( \pi_{study} \) is accounting for the autocorrelation among observations within each study; and \( \varepsilon \) 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 \( w_i \) 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 \( w_i \) 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 \( (e^{lnRR} - 1) \times 100\% \).

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

\[ P_{\alpha} = \left( \frac{R_s}{R_{s \alpha}} \right)^{\beta_1 + \beta_2 T} \]  

where \( P_{\alpha} \) is the proportion of remaining carbon attributes under \( \alpha \% \) 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
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

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**Figure 2.** The effects of plant mixtures on carbon attributes in relation to species richness, experimental duration, and experimental type (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 $\beta_1$, $\beta_2$, and $\beta_3$ in equation (3), respectively) are mean ±95% confidence intervals.
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...
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 Géback 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.

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.
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.

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Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://figshare.com/s/d010fedc1d9987a2231a.

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