

Plant diversity decreases greenhouse gas emissions by increasing soil and plant carbon storage in terrestrial ecosystems

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Abstract

The decline in global plant diversity has raised concerns about its implications for carbon fixation and global greenhouse gas emissions (GGE), including carbon dioxide (CO₂), nitrous oxide (N₂O) and methane (CH₄). Therefore, we conducted a comprehensive meta-analysis of 2103 paired observations, examining GGE, soil organic carbon (SOC) and plant carbon in plant mixtures and monocultures. Our findings indicate that plant mixtures decrease soil N₂O emissions by 21.4% compared to monocultures. No significant differences occurred between mixtures and monocultures for soil CO₂ emissions, CH₄ emissions or CH₄ uptake. Plant mixtures exhibit higher SOC and plant carbon storage than monocultures. After 10 years of vegetation development, a 40% reduction in species richness decreases SOC content and plant carbon storage by 12.3% and 58.7% respectively. These findings offer insights into the intricate connections between plant diversity, soil and plant carbon storage and GGE—a critical but previously unexamined aspect of biodiversity–ecosystem functioning.

KEYWORDS

carbon dioxide, carbon fixation, methane, nitrous oxide, plant mixtures

INTRODUCTION

The interface between the atmosphere and terrestrial biosphere is vital for carbon (C) exchange (Galy et al., 2015). Previous research shows that the loss of plant diversity can have comparable effects on ecological processes as other driving forces of global environmental change, such as drought or elevated carbon dioxide (CO_2 ; Cardinale et al., 2012; Duffy et al., 2017; Hooper et al., 2012), and thus the potential to affect the global C cycle. Plant diversity is a key driver of soil and plant C dynamics (Chen et al., 2023; Isbell et al., 2017), which, in turn, influences greenhouse gas emissions (GGE) (Loreau et al., 2023). However, the relationship between biodiversity and ecosystem functioning in this context has not previously been explored.

The emission of greenhouse gases, including CO_2 , nitrous oxide (N_2O) and methane (CH_4), is responsible for about 90% of anthropogenic warming (Kamman et al., 2012). These emissions are strongly influenced by environmental conditions but may also be related to plant diversity through its effects on plant and soil C pools. Specifically, research indicates that compared to monocultures, plant mixtures have beneficial effects on soil fertility, such as soil organic carbon (SOC), plant litter and microbial activity, with these positive effects becoming more pronounced with higher plant species richness and plot age (duration in an experimental plot or the estimated age of a non-experimental plot), leading to increased soil CO_2 emissions (Chen et al., 2019; Peng & Chen, 2021). Moreover, plant mixtures can boost plant productivity, facilitating greater uptake of soil nitrate nitrogen (NO_3^-) and reducing soil N_2O emissions (Furey & Tilman, 2021). These effects of plant diversity may interact with environmental conditions, particularly soil moisture, to influence CH_4 fluxes, which involves the activity of methanogenic and methane-oxidizing bacteria (Feng et al., 2020; Tate, 2015; Zhou, Zhang, et al., 2021; Zhou, Zuo, & Smaill, 2021). Wetland soils, characterized by high moisture and methanogenic bacteria dominance, tend to emit CH_4 , whereas well-aerated soils in forests and grasslands often serve as CH_4 sinks (Feng et al., 2020; Zhou, Zhang, et al., 2021). Increased plant residues, root exudates and microbial metabolites in mixed plant communities provide additional C substrates (Han et al., 2019; Zelnik & Carni, 2013), potentially elevating CH_4 emissions. Nitrogen (N) deposition, drought and soil type can also influence soil N and water availability (Lubbers et al., 2011; Smith et al., 2000) and plant growth, thereby modifying the effects of plant mixtures on GGE. For instance, N deposition could enhance plant litter inputs and accelerate plant litter decomposition, generating diverse C and N substrates that promote CO_2 , N_2O and CH_4 emissions (Chang et al., 2014; Niklaus et al., 2016).

Prior meta-analyses have focused on the effects of plant mixtures on plant productivity, C, N storage and microbial biomass (Chen et al., 2020, 2021; Chen & Chen, 2019, 2021). However, there remains a gap in understanding how C fluxes between soil, plants and the atmosphere may affect GGE differently between plant mixtures and monocultures. We compiled a comprehensive dataset from 272 papers, encompassing 2103 paired soil C, plant C and GGE measurements in plant mixtures and corresponding monocultures to address this gap (Table S1). Building upon existing knowledge, we hypothesize that (1) increased plant species richness and plot age enhance soil C content and plant growth (quantified by plant C), stimulating CO_2 and CH_4 emissions while reducing N_2O emissions, conversely, species loss will have the opposite effects; (2) environmental variables such as N application, soil type and aridity influence the effects of plant mixtures on plant and soil C storage and GGE.

MATERIALS AND METHODS

Data collection

We used the Web of Science (<https://www.webofscience.com/wos/alldb/basic-search>), Google Scholar (<http://scholar.google.com>) and China National Knowledge Infrastructure (<https://www.cnki.net>) to search for published papers up to 1 September 2023 using the search terms (“species diversity” OR “species richness” OR “species mixture” OR “intercrop” OR “pure” OR “polyculture” OR “monoculture”) AND (“greenhouse gas” OR “carbon dioxide” OR “ CO_2 ” OR “nitrous oxide” OR “ N_2O ” OR “methane” OR “ CH_4 ”) AND (“soil carbon”) AND (“plant carbon” OR “aboveground carbon” OR “belowground carbon” OR “shoot carbon” OR “root carbon” OR “litter carbon” OR “leaf carbon”). The search followed the “Preferred Reporting Items for Systematic Reviews and Meta-Analyses” (PRISMA) protocol (Moher et al., 2009; Figure S1). The identified publications were screened to meet the following criteria: (1) study aimed to examine the effects of plant mixtures on GGE (CO_2 , N_2O or CH_4), SOC content (SOC mass per mass of dry soil), plant tissue C concentration or plant C storage (plant tissue C concentration multiplied by plant biomass); (2) included plant mixture treatments and corresponding monocultures (all species presented in mixtures; mostly manipulative experiments); (3) compared monocultures and mixtures from the same site; (4) monocultures and mixtures had the same plot age; (5) included plant species, plant density and replications. Data duplication was avoided, and plant mixtures with varying species numbers were considered distinct observations (Chen et al., 2020). Most studies that met these criteria were manipulative experiments (Table S1), but we also identified a few studies that

compared naturally assembled plant communities (e.g. Díaz-Pinés et al. (2014); see Table S1). In cases where data were presented only in figures, we used Engauge Digitizer (Free Software Foundation, Inc., Boston, MA, USA) to extract data. For each study and species richness level, we extracted the mean, standard deviation/standard error (where available), and number of replicates for GGE (CO_2 , N_2O , CH_4), SOC content and plant C concentration and storage (included aboveground and root part).

From each paper, we also extracted measures of plant species richness, plot age, soil type (FAO), soil depth (midpoint of soil depth interval; Chen et al., 2020), ecosystem type (cropland, grassland, planted forest, natural forest, wetland), N fertilizer application (yes/no), plant group (legume/no legume), plant C parts (e.g. aboveground, root), technical method (e.g. for CO_2 , infrared gas analyser and gas chromatography; for soil C, elemental analyser and $\text{K}_2\text{Cr}_2\text{O}_7$ method), latitude, longitude and country. Additionally, we collected data on soil NO_3^- , NH_4^+ and total available inorganic nitrogen ($\text{NO}_3^- + \text{NH}_4^+$) in monoculture and plant mixtures from identified publications meeting the above criteria. Mean annual temperature (MAT°C) was also extracted from the paper or interpolated from the WorldClim version 2 dataset (Fick & Hijmans, 2017) when not provided, while the aridity index (calculated by the ratio of the mean annual precipitation to mean annual potential evapotranspiration; low values for arid soils and high values for wet soils) was obtained from the Global Aridity and PET Database (Zomer et al., 2008). In total, metadata were obtained from 272 articles with 2103 observations spanning 39 countries (Table S1). Figure 1 shows the distribution of study sites.

Data analysis

Relative effect size measurement

We tested the effect of plant mixtures on GGE, SOC and plant C concentration/storage compared to monocultures. We subsequently analysed whether the effect of plant mixtures was influenced by species richness, plot age and environmental conditions. For each observation (GGE, SOC and plant C concentration/storage (the aboveground and root plant C concentration and storage were analysed respectively)), we estimated the effect size of plant mixtures relative to monocultures using the natural log of the response ratio ($\ln\text{RR}$; Hedges et al., 1999) calculated according to Equation (1) and (2):

$$\ln\text{RR} = \ln(X_i) - \ln(X_c) = \ln(X_i / X_c) \quad (1)$$

$$X_c = \sum_{i=1}^n (p_i \times m_i) \quad (2)$$

where X_i is the observed value in a mixture, X_c is the expected value based on the weighted average of the component species in monoculture (eliminating the selection effect, retaining the complementarity effect) (Loreau & Hector, 2001), n is the number of component species in monoculture and p_i and m_i are the proportional density in mixtures and the observed value in monoculture of species i respectively.

As not all studies provided standard errors, we could not calculate the sampling variances for response variables. Therefore, we used the number of replicates for weighting associated with each $\ln\text{RR}$ observation (Balvanera et al., 2006; Chen et al., 2019, 2021; Chen & Chen, 2021):

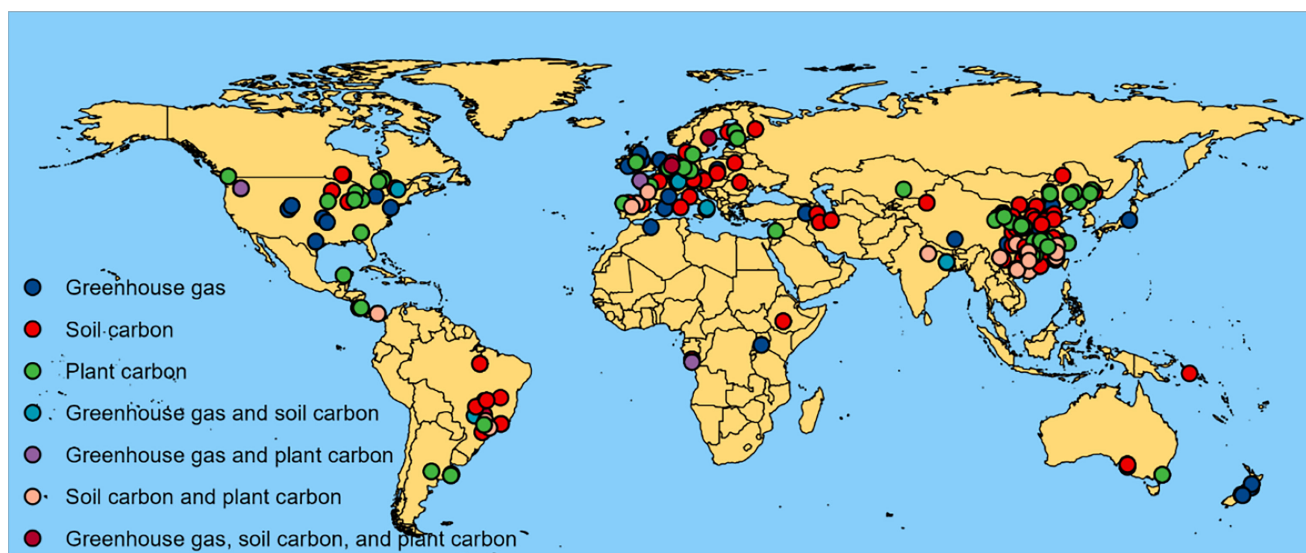


FIGURE 1 Sample sites of plant diversity studies testing the effects of plant mixtures on greenhouse gas emissions and plant and soil carbon sequestration used in the meta-analysis.

$$W_r = (N_c \times N_t) / (N_c + N_t) \quad (3)$$

where W_r is the weight associated with each $\ln RR$ observation, N_c is the number of replications in monoculture and N_t is the number of replications in plant mixtures.

We performed 9999 iterations of bootstrapping using MetaWin 2.1 software to generate 95% confidence intervals (CI) and weighted mean effect sizes ($\ln RR$) (Rosenberg et al., 2000).

Model selection

Plants in pot experiments often undergo controlled temperature and soil moisture adjustments, differing from the natural conditions experienced by plants in the field. Consequently, accurately determining the effects of mean annual temperature and aridity index for these experiments is not possible. Thus, we excluded pot data from our meta-regression analysis to explore the effects of species richness, plot age and other environmental variables on the response of GGE, SOC and plant C concentration/storage to the mixtures. We fitted the meta-regression with a mixed-effects regression model, separately analysing mixture effect sizes for CO_2 , N_2O , CH_4 emissions, CH_4 uptake, SOC content, plant C concentration and plant C storage. We evaluated linear and logarithmic functions to assess potential relationships between individual predictors (species richness, plot age, soil depth) and $\ln RR$; logarithmic species richness and plot age had lower (or similar) AIC values than linear species richness and plot age, while linear soil depth had lower AIC values than logarithmic soil depth (Table S3). Based on these findings, we used logarithmic species richness (R), logarithmic plot age (A), linear soil depth (D, specifically for SOC content) and environmental covariates (E, ecosystem type, mean annual temperature and aridity index) as fixed-effect terms in Equation (4). Additionally, to address variations between different studies, we incorporated a random effects term in Equation (4) to account for autocorrelation among observations.

$$\begin{aligned} \ln RR = & \beta_0 + \beta_1 \ln(R) + \beta_2 \ln(A) + \beta_3 D + \beta_4 E \\ & + \beta_5 \ln(R) \times \ln(A) + \beta_6 \ln(R) \times D + \beta_7 \ln(R) \times E \\ & + \beta_8 \ln(A) \times D + \beta_9 \ln(A) \times E + \beta_{10} D \times E \\ & + \beta_{11} \ln(R) \times \ln(A) \times D + \beta_{12} \ln(R) \times \ln(A) \times E \\ & + \beta_{13} \ln(R) \times D \times E + \beta_{14} \ln(A) \times D \times E \\ & + \beta_{15} \ln(R) \times \ln(A) \times D \times E + \pi_{\text{study}} + \epsilon \end{aligned} \quad (4)$$

where β and ϵ are the coefficient and sampling error, respectively, and π_{study} are random effects accounting for the potential effects of variation at different study sites. The *nlme* package was used for the analysis with varFunc ($\sim 1/W_r$) as weights (W_r = weight associated with each $\ln RR$ observation) and lmeControl (sigma = 1) to fix the scale parameter (Heisterkamp et al., 2017; Pinheiro et al., 2017). We

scaled all predictors (observed values minus mean, divided by standard deviation), including species richness, plot age and soil depth (Cohen et al., 2014).

To prevent overfitting in Equation (4), the most parsimonious model selected from all alternative models was selected using the ‘dredge’ function of the muMIn package by comparing AICs (Barton, 2009). Potential models were defined as those models with a $\Delta\text{AIC} \leq 2$ compared to the best model with the highest weight value. If these potential models included species richness, plot age and their interaction, we prioritized retaining these variables as they aligned with our core hypotheses for evaluating the effects of species richness and plot age in plant mixtures. Terms including E were excluded in the final parsimonious models of Equations (5) and (6). Equation (5) was used to determine the $\ln RR$ for CO_2 emissions, N_2O emissions, CH_4 emissions, CH_4 uptake and plant C concentration and storage, and Equation (6) was used for SOC content.

$$\ln RR = \beta_0 + \beta_1 \ln(R) + \beta_2 \ln(A) + \beta_3 \ln(R) \times \ln(A) + \pi_{\text{site}} + \epsilon \quad (5)$$

$$\ln RR = \beta_0 + \beta_1 \ln(R) + \beta_2 \ln(A) + \beta_3 D + \beta_4 \ln(R) \times \ln(A) + \beta_5 \ln(A) \times D + \pi_{\text{site}} + \epsilon \quad (6)$$

The *car* package was used to calculate variance inflation factors (VIF) (Fox et al., 2007), and Egger's regression test was used to evaluate publication bias. We did not find a multicollinearity problem in any model, with all factors having VIFs < 2 (Table S1), nor did we find any significant publication bias based on Egger's regression (Table S4). We used Shapiro–Wilk's test on the final model residuals in Equations (5) and (6), and found that the final models deviated from the normality assumption. Therefore, we bootstrapped the fitted coefficients by 1000 iterations with the *lmeresampler* package. In addition, we obtained marginal and conditional R^2 values and estimates and p-values for explanatory variables (Table S1).

The effect size measure $\ln RR$ was converted into a percentage change to facilitate the interpretation of results:

$$(e^{\ln RR} - 1) \times 100\% \quad (7)$$

Measurement of species loss effects

We focused particularly on the interaction effects between species richness and plot age, as these are crucial drivers of ecosystem functioning under plant mixtures. When we found a significant interaction between species richness and plot age, we provided a more easily interpretable illustration of the potential effects of plant species richness losses on our mixture effect size response variables. We aimed to determine the effect of species richness on mixture effect sizes while accounting for its interaction with plot age. We assumed that R_1 was the maximum species richness observed in our dataset (64; Table S1), and R_α represented plant species richness after a percentage of α of species richness loss from the

maximum (e.g. 50% species richness loss corresponds to $R_\alpha = 32$). We incorporated R_1 and R_α into Equations (5) and (6) to obtain the largest effect size for response variables under maximum species richness ($\ln RR_1$) and after species richness loss ($\ln RR_\alpha$). Using $\ln RR_\alpha$ and $\ln RR_1$, we calculated the remaining effect size after species richness loss (Chen et al., 2019, 2021) as follows:

$$\ln RR_\alpha - \ln RR_1 = (\beta_1 + \beta_5 \ln(A)) \times (\ln R_\alpha - \ln R_1) \quad (8)$$

$$\ln(RR_\alpha / RR_1) = \ln\left((R_\alpha / R_1)^{\beta_1 + \beta_5 \ln(A)}\right) \quad (9)$$

We removed the natural log of Equation (9) and set X_{t-1} and X_{t-a} as the observed values for maximum species richness and $\alpha\%$ loss of maximum species richness in a mixture respectively. The response ratio (RR) is X_t divided by X_c . Assuming that X_c did not change with species loss, we obtained Equation (10) (Chen et al., 2019, 2021):

$$P_\alpha = RR_\alpha / RR_1 = (X_{t-a} / X_c) / (X_{t-1} / X_c) = (R_\alpha / R_1)^{\beta_1 + \beta_5 \ln(A)} \quad (10)$$

where P_α is the proportion of remaining greenhouse gases, SOC content or plant C concentration and storage and RR_α and RR_1 are the response ratio of the effect of plant mixtures relative to monoculture with $\alpha\%$ loss of maximum species richness and no loss of maximum species richness respectively.

Effects of environmental covariates

To further test the effects of environmental covariates (E) on GGE, SOC and plant C concentration or storage, we modelled the mixture effect sizes as follows:

$$\ln RR = \beta_0 + \beta_1 E + \pi_{site} + \epsilon \quad (11)$$

where E included ecosystem type, mean annual temperature, aridity index, soil type, plant parts, N application, plant group and technical method (Table S2). All statistical analyses were performed in R 4.1.1 (R Core Team, 2013).

RESULTS

The comparison between plant mixtures and monocultures revealed notable differences in GGE fluxes, soil C and plant C, irrespective of species richness in the mixture. Specifically, plant mixtures (with a species richness range of 2–64) had 21.4% lower N_2O emissions than average monocultures, but 3.1%, 3.8% and 11.2% higher SOC content ($g\ kg^{-1}$ soil), plant C concentration and plant C storage respectively (Figure 2). No significant differences in CO_2 emissions, CH_4 emissions and CH_4 uptake were observed between plant mixtures and monocultures.

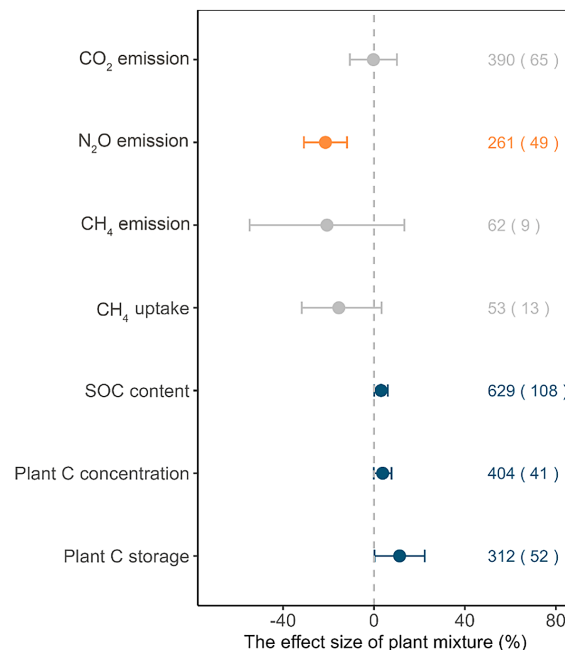


FIGURE 2 Mixture effect sizes (log-response ratios of plant mixtures relative to monoculture averages) on carbon dioxide (CO_2) emissions, nitrous oxide (N_2O) emissions, methane (CH_4) emissions, CH_4 uptake, soil organic carbon (SOC) content and plant community C (carbon) concentration and storage. CH_4 emission data were derived from wetland ecosystems, while CH_4 uptake data were derived from grassland, farmland and forest ecosystems. Dots and horizontal error bars represent means and 95% confidence intervals for plant mixture effects when compared to the averages for monocultures. Colours in orange, blue and grey indicate a decrease, increase and insignificant values respectively. The number of observations is shown, with the number of studies in parentheses.

No significant relationships occurred between species richness and the effect sizes of mixtures on N_2O emissions, CH_4 emissions or CH_4 uptake, indicating no further changes with increasing species richness beyond the transition from monocultures to mixtures (Table S1). However, species richness did enhance mixture effect sizes on CO_2 emissions and SOC content from zero in species-poor mixtures to positive in species-rich mixtures (Figure 3; Table S1). Plot age did not significantly impact mixture effect sizes on CH_4 emissions, CH_4 uptake, plant C concentration and plant C storage (Table S1). However, plot age did increase mixture effect sizes on CO_2 emissions, N_2O emissions and SOC content (Figure 3; Table S1). That is, for each of these variables, the difference between monocultures and mixtures was larger on average in older plots. Upon dividing plant species richness into four groups (2, >2–5, >5–10, >10), higher species richness consistently increased CO_2 emissions, SOC content and plant C storage (Figure S4), affirming the robustness of these findings. The impact of plant species richness on plant C concentration could not be assessed because data on plant C concentration almost exclusively came from monocultures and two-species mixtures.

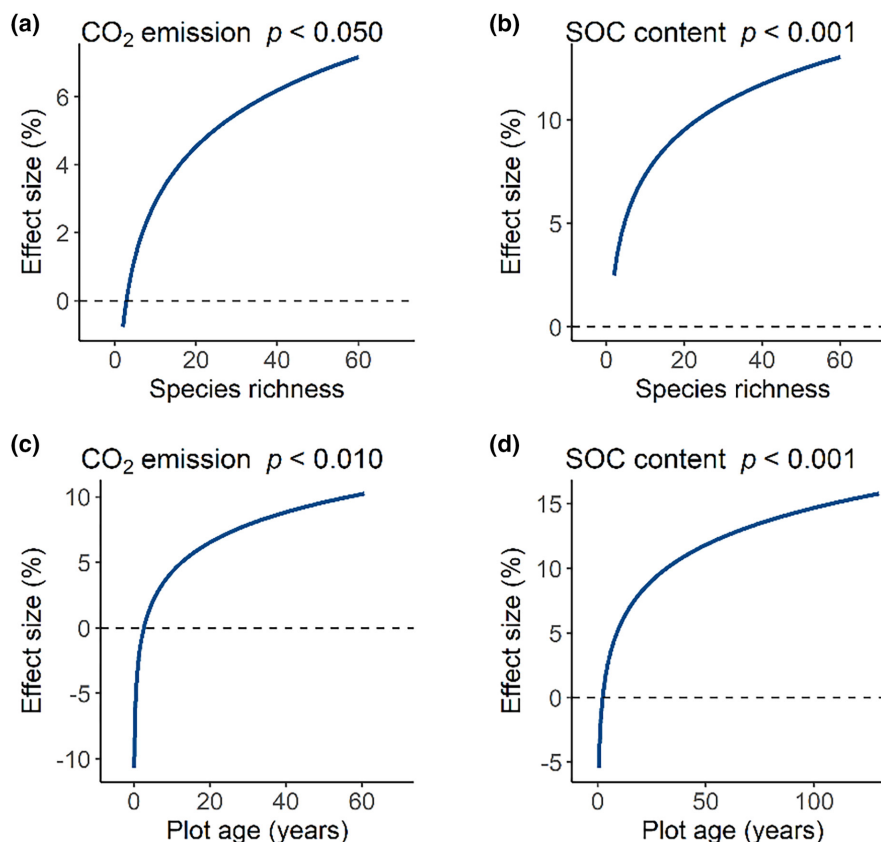


FIGURE 3 Mixture effect sizes (log-response ratios of plant mixtures relative to monoculture averages) on carbon dioxide (CO₂) emissions and soil organic carbon (SOC) content in relation to single variables: (a) CO₂ emissions–species richness, (b) SOC content–species richness, (c) CO₂ emissions–plot age, (d) SOC content–plot age. The influence of single variables on the mixture effect sizes was derived from Equations (5) and (6) in the Methods section.

Plot age and soil depth affected some of these relationships. For example, mixture effect sizes on SOC content and plant C storage increased more with species richness in older plots compared to younger ones (Figure 4a,b; Table S1). The interaction between soil depth and plot age significantly affected mixture effect sizes for SOC content, indicating a more pronounced positive effect of plant mixtures on SOC content in deeper soils with increasing plot age (Figure 4c; Table S1). N application resulted in larger mixture effect sizes on CO₂, N₂O and CH₄ emissions compared to scenarios with no N addition (Figure 5a–d). There was a positive correlation between mixture effect sizes on CO₂ emissions and mixture effect sizes on SOC content, while positive correlations were observed between mixture effect sizes on soil NO₃[−] and mixture effect sizes on N₂O emissions (Figure 5e,f). Additionally, mixture effect sizes on CH₄ emissions were negative under high aridity (low aridity index) but approached zero at low aridity (high aridity index; Figure 5g). Mixture effect sizes on GGE, SOC and plant C concentration or storage did not significantly differ across different ecosystem types, annual average temperatures, plant types (presence or absence of legumes), technical methods, plant parts or soil types (Table S2). However, Eutric Fluvisols had significantly

larger mixture effect sizes on plant C storage than other soil types (Figure S3).

Due to the unavailability of SOC content data for the entire soil depth profile and potential differences in soil depth between monocultures and mixtures, we did not calculate the absolute effects of mixtures on SOC storage. However, based on our predictions, a 40% reduction in species richness in forests and grasslands decreased SOC content and plant C storage by 3.12% and 8.41% after 1 year and 12.3% and 58.7% after 10 years respectively. Similarly, a 60% decrease in species richness (from 100% to 40%) decreased SOC content and plant C storage by 4.38% and 8.91% after 1 year and 17.0% and 61.3% after 10 years respectively (Figure 6).

DISCUSSION

Effect of plant mixtures on soil carbon

Experiments and observational studies over the last 30 years have shown that plant diversity often has strong effects on vegetation biomass and productivity across a range of ecosystem types (Chen et al., 2023; Huang et al., 2018; Isbell et al., 2017; Tilman et al., 1996). Our results show that these

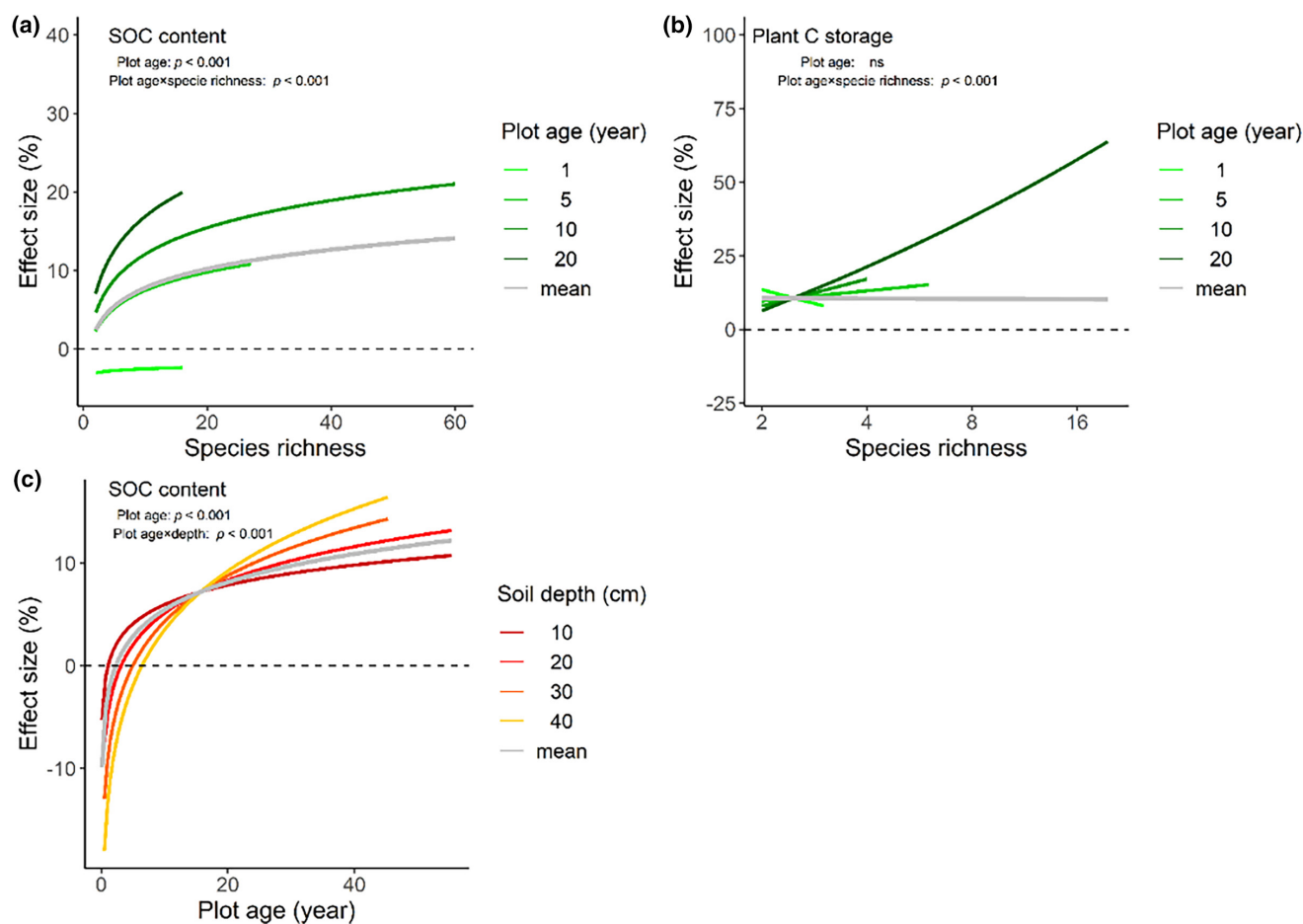


FIGURE 4 Mixture effect sizes (log-response ratios of plant mixtures relative to monoculture averages) on soil organic carbon (SOC) content and plant community carbon (C) storage in relation to two interacting variables: (a) SOC content–species richness $\times$ plot age, (b) plant C storage–species richness $\times$ plot age, (c) SOC content–plot age $\times$ soil depth. The influence of the two interacting variables on mixture effect sizes was derived from Equations (5) and (6) in the Methods section. ns indicates $p > 0.05$.

plant diversity effects also translate to important processes affecting climate, namely the storage of C in soils and emissions of greenhouse gases. Plant species mixtures have higher SOC contents than monocultures, with plant species richness, plot age and soil depth modifying this effect (see Figures 2 and 4). This finding highlights the crucial role of plant diversity in maintaining soil C reservoirs, a factor also affected by various environmental parameters. Soil C is more than three times that of plants and the atmosphere (Hicks Pries Hicks Pries Caitlin et al., 2017), emphasizing the importance of even slight changes in SOC for global GGE dynamics (Chen et al., 2018). Compared to monocultures, plant mixtures enhance C inputs to soils through litter decomposition and root exudation, contributing to increased soil C content (Chen et al., 2018, 2020). This process is crucial in absorbing atmospheric CO_2 and mitigating climate change. However, our inability to quantify the absolute amounts of SOC per unit area due to insufficient data on soil depth and soil bulk density poses a limitation. The positive correlation between species richness and SOC content is consistent with the well-established relationship between higher species richness and increased plant productivity (Balvanera

et al., 2006; Hector et al., 1999; Spehn et al., 2000; Tilman et al., 1996; Van Ruijven & Berendse, 2005). Enhanced productivity results in greater C export from plant residues to soil, elevating SOC content (Chen et al., 2020; Liu et al., 2018). Moreover, the influx of plant root exudates and litter into the soil tends to increase with plot age (Chen et al., 2020; Forrester et al., 2013), further augmenting SOC content over time. These processes likely help explain our finding of higher SOC in more diverse plant plots.

Effect of plant mixtures on plant carbon

Plant mixtures exhibit higher plant C concentrations and storage than monocultures, with the magnitude of the mixture effect on plant C storage positively correlating with the species richness of mixtures and plot age (see Figures 2 and 4b). This indicates a progressive increase in the capture of atmospheric CO_2 over time by more species-rich plant communities. The underlying mechanism for this phenomenon may lie in the higher community leaf area index observed in plant mixtures (Ibanez et al., 2021),

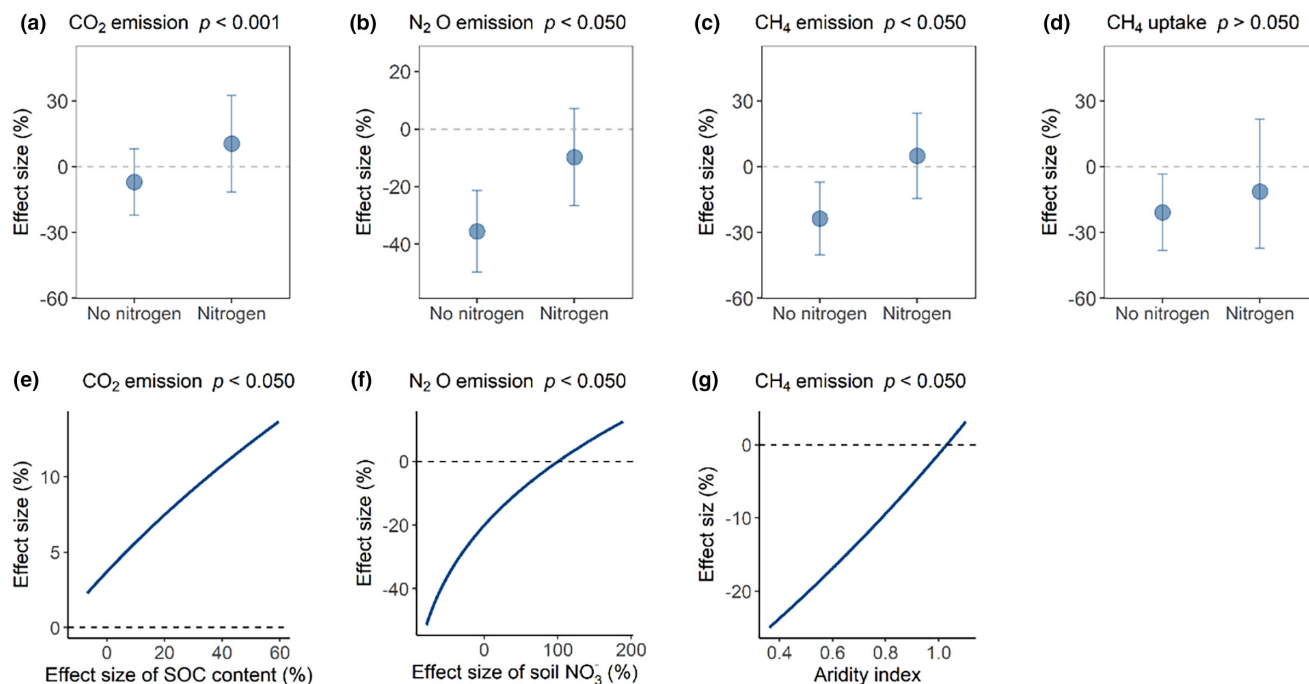


FIGURE 5 Mixture effect sizes (log-response ratios of plant mixtures relative to monoculture averages) on carbon dioxide (CO₂) emissions, nitrous oxide (N₂O) emissions, methane (CH₄) emissions and uptake in relation to nitrogen fertilizer application (No nitrogen vs. Nitrogen; a–d), in relation to mixture effect sizes on soil organic carbon (SOC) content (e) and soil nitrate nitrogen (NO₃⁻) (f), and in relation to aridity index (high values less arid conditions; g) CH₄ emissions data were derived from wetland ecosystems, while CH₄ uptake data were derived from grassland, farmland and forest ecosystems. Dots and vertical error bars in panels a–d represent means and 95% confidence intervals respectively.

enhancing light interception (Manevski et al., 2017) and photosynthetic rates (Dong et al., 2004), ultimately facilitating plant C concentration and storage (Veryard et al., 2023). The complementarity of resource use among species has been proposed as a key driver of increased productivity in species-rich, decade-old grassland ecosystems (Van Ruijven & Berendse, 2005). With plot age increasing, plant communities with higher species richness tend to accumulate more plant biomass by absorbing CO₂ and soil nutrients, such as N and phosphorus, subsequently increasing plant C storage (Furey & Tilman, 2021; Klironomos et al., 2000; Siemann, 1998; Tilman et al., 1996).

Soil type can also influence the response of plant C storage to plant species richness. For example, Eutric Fluvisols, characterized by higher nutrient content (N and phosphorus) than other soil types (Nachtergaele et al., 2009), show greater mixture effects on plant C storage than Dystric Cambisols, Ferralic Arenosols and Ferralsols (see Table S2, Figure S3). In these nutrient-rich soils (e.g. Eutric Fluvisols), plant mixtures would promote C fixation through photosynthesis, increasing plant C storage (Chen & Chen, 2021; Forrester & Bauhus, 2016).

Effect of plant mixtures on greenhouse gas emissions

The effect of plant mixtures on emissions varies across different greenhouse gases. Soil N₂O emissions are 21.4%

lower in plant mixtures than monocultures (see Figure 2), indicating a beneficial influence of plant mixtures on mitigating N₂O emissions. This reduction is attributed to the decrease in soil NO₃⁻ levels in plant mixtures (see Figure 5), as soil NO₃⁻ is a precursor to N₂O emissions (Han et al., 2019). Plant mixtures absorb more available soil NO₃⁻ than monocultures (Furey & Tilman, 2021), potentially explaining the observed decrease in N₂O emissions (see Figure 2). In contrast with hypothesis, the increase in plant species richness within mixtures does not lead to further reductions in N₂O emissions (see Table S1), possibly due to the lack of statistical power as most mixtures in our dataset have low species richness, or to a balance between NO₃⁻ absorption and N mineralization with increasing plant species richness. Increasing species richness in plant mixtures can also increase soil NO₃⁻ absorption (Furey & Tilman, 2021). Moreover, plant mixtures accumulate soil total N, improving N mineralization and increasing NO₃⁻ production (Chen et al., 2021, 2023). Thus, NO₃⁻ absorption and production may reach an equilibrium. Furthermore, the build-up of total N in soil under long-term plant mixtures could promote soil NO₃⁻ production (Chen et al., 2021), which may explain the observed positive correlation between plot age and mixture effect size on N₂O emissions in our study (see Table S1).

While soil CO₂ emissions do not increase on average under plant mixtures, higher plant species richness and older plots are associated with positive effects of

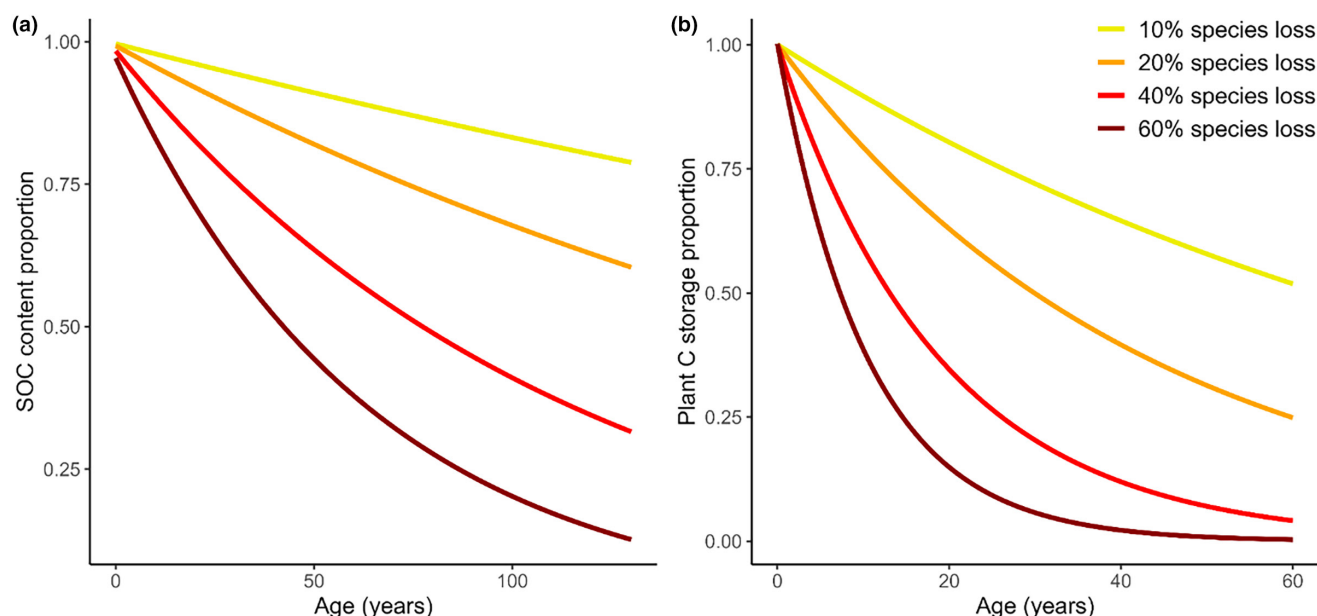


FIGURE 6 Predicted responses of (a) soil organic carbon (SOC) content and (b) plant community carbon (c) storage to reductions in species richness at establishment.

plant mixtures on soil CO_2 emissions. However, the higher plant species richness and older plots are likely correlated with high CO_2 uptake, reflected in the high plant and soil C storage (Figure 3). The increased C would stimulate microbial activity (Chen et al., 2019) and CO_2 emissions (Chen & Chen, 2019). Thus, the increased soil CO_2 emissions in species-rich, old plots do not necessarily reflect increased net CO_2 emissions, as it may be offset by increased CO_2 uptake through photosynthesis or other mechanisms. One study reports that the positive effect of plant mixtures on SOC content and subsequent increase in SOC decomposition only partially offset the positive impact of species richness on CO_2 uptake (Stocker et al., 1999). In our study, the positive effect of mixtures on SOC is relatively larger than the positive effect on CO_2 emissions in species-rich, old plots (see Figures 4a,b and 5), suggesting a potentially negative effect of plant species richness and plot age on net CO_2 emissions for these ecosystems.

Overall, plant mixtures have similar CH_4 emission and uptake levels as monocultures, independent of species richness in mixtures and plot age. This minimal impact of plant mixtures on soil CH_4 sources and sinks contradicts our hypothesis. However, a review focusing on constructed wetlands also reports a negligible overall impact of mixtures on soil CH_4 emissions (Maucieri et al., 2017). Additionally, alterations in microbial community structure associated with CH_4 emissions under plant mixtures are not contingent upon variations in plant species richness (Maucieri et al., 2017; Zhang et al., 2010). Nonetheless, further research is needed to elucidate the mechanisms governing the response of soil CH_4 emissions and uptake to plant

mixtures (see Figure 2; Table S1). We find a positive relationship between effect of mixtures on CH_4 emissions and aridity index, indicating that plant mixtures are more conducive to promoting CH_4 emissions under more humid conditions. A recent study reveals that plant mixtures exhibit enhanced productivity in humid regions (Jactel et al., 2018), potentially stimulating increased litterfall and elevating the amount of substrate for CH_4 emissions.

Growing N pollution is another major axis of global change (Matson et al., 2002). We find that N addition enhances the mixture effects on CO_2 , N_2O and CH_4 emissions (see Figure 5a–c), consistent with earlier findings that N fertilization can alleviate soil nutrient deficiencies, providing better support for the growth of plant mixtures (LeBauer & Treseder, 2008). Enhanced N utilization by plant mixtures facilitates the contributions of plant litter and root exudates to soil fertility (Barneze et al., 2020; Niklaus et al., 2016), and intensified root-driven nutrient mineralization intensifies the production of N and amino acids (Barneze et al., 2020; Chang et al., 2014), precursors for CO_2 , N_2O and CH_4 , and thus promoting GGE. Therefore, mitigating N deposition in natural ecosystems may be beneficial for offsetting GGE.

Implications for potential consequences of climate change

The insights from experimental biodiversity studies, like the German Jena Experiment and the US BioDIV project, are considered reliable for understanding real-world ecosystems (Jochum et al., 2020). Small-scale

investigations into the impact of plant diversity on soil C and N (Chen et al., 2020, 2021), supported by evidence from larger natural ecosystems (Chen et al., 2023), suggest that meta-analyses of such experiments can offer valuable insights into factors influencing global-scale GGE. As ecosystem services and functioning are linked directly to plant diversity (Isbell et al., 2015), our study's findings underscore the potential of preserving and promoting plant diversity as a nature-based solution for mitigating climate change consequences, similar to Mori et al. (2021). The consistent effects of plant mixtures on GGE, soil C and plant C fixation across various ecosystem types and environmental conditions, such as soil type, aridity and temperature, support the general validity of these findings. Similar studies have reported the consistent influence of plant mixtures on aboveground and belowground plant biomass (Ma & Chen, 2016; Zhang et al., 2012), soil microbial biomass (Chen et al., 2019), soil N (Chen et al., 2021) and phosphorus (Chen et al., 2022) across diverse ecosystem types and environmental conditions. However, increases in species richness within mixtures and plot age amplify the effects of plant mixture effects on C fluxes in ecosystems, further emphasizing the importance of long-term preservation of plant diversity for climate change mitigation.

The observed decline in C storage when converting plant mixtures to monocultures raises concerns. Estimated global SOC decreases by 25% following the conversion of forests to cropland, resulting in a 32% increase in C emissions (Don et al., 2011). Human-induced habitat destruction and loss of plant diversity exacerbate global C emissions (Isbell et al., 2015; Portner et al., 2023). Our findings highlight that even a moderate (40%) decrease in plant species richness over a decade in forests and grasslands could lead to substantial losses in SOC content (12.3%) and plant C storage (58.7%) over the course of decades (Figure 6). Given the ongoing global decline in plant diversity (Butchart et al., 2010), terrestrial ecosystems are at risk of losing C storage capacity, particularly as plot age increases.

CONCLUSION

Our study synthesizes existing data on the role of plant diversity in regulating soil and plant C storage and, consequently, its impact on GGE. We find that plant mixtures decrease soil N₂O emissions relative to average monocultures while enhancing soil and plant C storage. The widespread cultivation of plant monocultures threatens the mitigation capacity of terrestrial ecosystems in the face of climate change. Preserving species richness and older ecosystems emerges as a crucial strategy to increase C storage and reduce GGE. Furthermore, our analysis offers valuable insights for refining land surface models to predict global C cycles and GGE more accurately.

AUTHOR CONTRIBUTIONS

X.Q. designed the study. P.D., M.Z., S.W., X.H., L.L., T.H. and C.W. collected data. P.D., X.Q., X.C., M.L., J.E.D., X.L., K.H.M.S. and B.S. contributed to discussing the analysis and results and to writing, and editing the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data supporting the results used to generate the analyses are archived in Zenodo (<https://zenodo.org/doi/10.5281/zenodo.10393551>). The data are also attached as supplementary information.

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REFERENCES

- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9, 1146–1156.
- Barneze, A.S., Whitaker, J., McNamara, N.P. & Ostle, N.J. (2020) Legumes increase grassland productivity with no effect on nitrous oxide emissions. *Plant and Soil*, 446, 163–177.
- Barton, K. (2009) *MuMIn: multi-model inference*.
- Butchart, S.H., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P., Almond, R.E. et al. (2010) Global biodiversity: indicators of recent declines. *Science*, 328, 1164–1168.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. et al. (2012) Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.
- Chang, J., Fan, X., Sun, H., Zhang, C., Song, C., Chang, S.X. et al. (2014) Plant species richness enhances nitrous oxide emissions in microcosms of constructed wetlands. *Ecological Engineering*, 64, 108–115.
- Chen, C., Chen, H.Y.H., Chen, X. & Huang, Z. (2019) Meta-analysis shows positive effects of plant diversity on microbial biomass and respiration. *Nature Communications*, 10, 1332.
- Chen, S., Wang, W., Xu, W., Wang, Y., Wan, H., Chen, D. et al. (2018) Plant diversity enhances productivity and soil carbon storage. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 4027–4032.
- Chen, X. & Chen, H.Y.H. (2019) Plant diversity loss reduces soil respiration across terrestrial ecosystems. *Global Change Biology*, 25, 1482–1492.
- Chen, X. & Chen, H.Y.H. (2021) Plant mixture balances terrestrial ecosystem C:N:P stoichiometry. *Nature Communications*, 12, 4562.

- Chen, X., Chen, H.Y.H. & Chang, S.X. (2022) Meta-analysis shows that plant mixtures increase soil phosphorus availability and plant productivity in diverse ecosystems. *Nature Ecology & Evolution*, 6, 1112–1121.
- Chen, X., Chen, H.Y.H., Searle, E.B., Chen, C. & Reich, P.B. (2021) Negative to positive shifts in diversity effects on soil nitrogen over time. *Nature Sustainability*, 4, 225–232.
- Chen, X., Taylor, A.R., Reich, P.B., Hisano, M., Chen, H.Y.H. & Chang, S.X. (2023) Tree diversity increases decadal forest soil carbon and nitrogen accrual. *Nature*, 620, E16.
- Chen, X.L., Chen, H.Y.H., Chen, C., Ma, Z.L., Searle, E.B., Yu, Z.P. et al. (2020) Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis. *Biological Reviews*, 95, 167–183.
- Cohen, P., West, S.G. & Aiken, L.S. (2014) *Applied multiple regression/correlation analysis for the behavioral sciences*. New York: Psychology Press.
- Díaz-Pinés, E., Schindlbacher, A., Godino, M., Kitzler, B., Jandl, R., Zechmeister-Boltenstern, S. et al. (2014) Effects of tree species composition on the CO₂ and N₂O efflux of a Mediterranean mountain forest soil. *Plant and Soil*, 384, 243–257.
- Don, A., Schumacher, J. & Freibauer, A. (2011) Impact of tropical land-use change on soil organic carbon stocks—a meta-analysis. *Global Change Biology*, 17, 1658–1670.
- Dong, S.K., Kang, M.Y., Hu, Z.Z., Long, R. & Pu, X.P. (2004) Performance of cultivated perennial grass mixtures under different grazing intensities in the alpine region of the Qinghai-Tibetan plateau. *Grass and Forage Science*, 59, 298–306.
- Duffy, J.E., Godwin, C.M. & Cardinale, B.J. (2017) Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature*, 549, 261–264.
- Feng, H., Guo, J., Han, M., Wang, W., Peng, C., Jin, J. et al. (2020) A review of the mechanisms and controlling factors of methane dynamics in forest ecosystems. *Forest Ecology and Management*, 455, 117702.
- Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.
- Forrester, D.I. & Bauhus, J. (2016) A review of processes behind diversity-productivity relationships in forests. *Current Forestry Reports*, 2, 45–61.
- Forrester, D.I., Pares, A., O'Hara, C., Khanna, P.K. & Bauhus, J. (2013) Soil organic carbon is increased in mixed-species plantations of eucalyptus and nitrogen-fixing acacia. *Ecosystems*, 16, 123–132.
- Fox, J., Friendly, G.G., Graves, S., Heiberger, R., Monette, G., Nilsson, H. et al. (2007) The car package.
- Furey, G.N. & Tilman, D. (2021) Plant biodiversity and the regeneration of soil fertility. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2111321118.
- Galy, V., Peucker-Ehrenbrink, B. & Eglinton, T. (2015) Global carbon export from the terrestrial biosphere controlled by erosion. *Nature*, 521, 204–207.
- Han, W., Luo, G., Luo, B., Yu, C., Wang, H., Chang, J. et al. (2019) Effects of plant diversity on greenhouse gas emissions in microcosms simulating vertical constructed wetlands with high ammonium loading. *Journal of Environmental Sciences*, 77, 229–237.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G. et al. (1999) Plant diversity and productivity experiments in European grasslands. *Science*, 286, 1123–1127.
- Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156.
- Heisterkamp, S.H., van Willigen, E., Diderichsen, P.-M. & Maringwa, J. (2017) *Update of the nlme package to allow a fixed standard deviation of the residual error*.
- Hicks Pries Caitlin, E., Castanha, C., Porras, R.C. & Torn, M.S. (2017) The whole-soil carbon flux in response to warming. *Science*, 355, 1420–1423.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E., Hungate, B.A., Matulich, K.L. et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486, 105–108.
- Huang, Y., Chen, Y., Castro-Izaguirre, N., Baruffol, M., Brezzi, M., Lang, A. et al. (2018) Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science*, 362, 80–83.
- Ibanez, M., Altimir, N., Ribas, A., Eugster, W. & Sebastia, M.T. (2021) Cereal-legume mixtures increase net CO₂ uptake in a forage crop system in the eastern Pyrenees. *Field Crops Research*, 272, 108262.
- Isbell, F., Adler, P.R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C. et al. (2017) Benefits of increasing plant diversity in sustainable agroecosystems. *Journal of Ecology*, 105, 871–879.
- Isbell, F., Tilman, D., Polasky, S. & Loreau, M. (2015) The biodiversity-dependent ecosystem service debt. *Ecology Letters*, 18, 119–134.
- Jactel, H., Gritti, E.S., Drössler, L., Forrester, D.I., Mason, W.L., Morin, X. et al. (2018) Positive biodiversity-productivity relationships in forests: climate matters. *Biology Letters*, 14, 20170747.
- Jochum, M., Fischer, M., Isbell, F., Roscher, C., van der Plas, F., Boch, S. et al. (2020) The results of biodiversity-ecosystem functioning experiments are realistic. *Nature Ecology & Evolution*, 4, 1485–1494.
- Kammann, C., Ratering, S., Eckhard, C. & Müller, C. (2012) Biochar and hydrochar effects on greenhouse gas (carbon dioxide, nitrous oxide, and methane) fluxes from soils. *Journal of Environmental Quality*, 41, 1052–1066.
- Klironomos, J.N., McCune, J., Hart, M. & Neville, J. (2000) The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. *Ecology Letters*, 3, 137–141.
- LeBauer, D.S. & Treseder, K.K. (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, 89, 371–379.
- Liu, X., Trogisch, S., He, J.S., Niklaus, P.A., Bruehlheide, H., Tang, Z. et al. (2018) Tree species richness increases ecosystem carbon storage in subtropical forests. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20181240.
- Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.
- Loreau, M., Jarne, P. & Martiny, J.B.H. (2023) Opportunities to advance the synthesis of ecology and evolution. *Ecology Letters*, 26, S11–S15.
- Lubbers, I.M., Brussaard, L., Otten, W. & Van Groenigen, J.W. (2011) Earthworm-induced N mineralization in fertilized grassland increases both N₂O emission and crop-N uptake. *European Journal of Soil Science*, 62, 152–161.
- Ma, Z. & Chen, H.Y.H. (2016) Effects of species diversity on fine root productivity in diverse ecosystems: a global meta-analysis. *Global Ecology and Biogeography*, 25, 1387–1396.
- Manevski, K., Laerke, P.E., Jiao, X.R., Santhome, S. & Jorgensen, U. (2017) Biomass productivity and radiation utilisation of innovative cropping systems for biorefinery. *Agricultural and Forest Meteorology*, 233, 250–264.
- Matson, P., Lohse, K.A. & Hall, S.J. (2002) The globalization of nitrogen deposition: consequences for terrestrial ecosystems. *Ambio*, 31, 113–119.
- Maucieri, C., Barbera, A.C., Vymazal, J. & Borin, M. (2017) A review on the main affecting factors of greenhouse gases emission in constructed wetlands. *Agricultural and Forest Meteorology*, 236, 175–193.
- Moher, D., Liberati, A., Tetzlaff, J. & Altman, D.G. (2009) Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS Medicine*, 6, e1000097.
- Mori, A.S., Dee, L.E., Gonzalez, A., Ohashi, H., Cowles, J., Wright, A.J. et al. (2021) Biodiversity-productivity relationships are key

- to nature-based climate solutions. *Nature Climate Change*, 11, 543–550.
- Nachtergaele, F., Velthuisen, H., Verelst, L., Wiberg, D.J.F. & Agriculture Organization of the United Nations, R. (2009) *Harmonized world soil database (hwsd)*.
- Niklaus, P.A., Le Roux, X., Poly, F., Buchmann, N., Scherer-Lorenzen, M., Weigelt, A. et al. (2016) Plant species diversity affects soil-atmosphere fluxes of methane and nitrous oxide. *Oecologia*, 181, 919–930.
- Peng, S. & Chen, H.Y.H. (2021) Global responses of fine root biomass and traits to plant species mixtures in terrestrial ecosystems. *Global Ecology and Biogeography*, 30, 289–304.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B. et al. (2017) Package 'nlme'. 3.
- Portner, H.O., Scholes, R.J., Arneth, A., Barnes, D.K.A., Burrows, M.T., Diamond, S.E. et al. (2023) Overcoming the coupled climate and biodiversity crises and their societal impacts. *Science (New York, N.Y.)*, 380, eabl4881.
- R Core Team. (2013) R: A language and environment for statistical computing.
- Rosenberg, M.S., Adams, D.C. & Gurevitch, J. (2000) *MetaWin. Statistical software for meta-analysis*. Version, 2.
- Siemann, E. (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, 79, 2057–2070.
- Smith, K.A., Dobbie, K.E., Ball, B.C., Bakken, L.R., Sitaula, B.K., Hansen, S. et al. (2000) Oxidation of atmospheric methane in northern European soils, comparison with other ecosystems, and uncertainties in the global terrestrial sink. *Global Change Biology*, 6, 791–803.
- Spehn, E.M., Joshi, J., Schmid, B., Diemer, M. & Körner, C. (2000) Above-ground resource use increases with plant species richness in experimental grassland ecosystems. *Functional Ecology*, 14, 326–337.
- Stocker, R., Körner, C., Schmid, B., Niklaus, P.A. & Leadley, P.W. (1999) A field study of the effects of elevated CO₂ and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Global Change Biology*, 5, 95–105.
- Tate, K.R. (2015) Soil methane oxidation and land-use change—from process to mitigation. *Soil Biology and Biochemistry*, 80, 260–272.
- Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718–720.
- Van Ruijven, J. & Berendse, F. (2005) Diversity-productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 695–700.
- Veryard, R., Wu, J., O'Brien, M.J., Anthony, R., Both, S., Burslem, D.F.R.P. et al. (2023) Positive effects of tree diversity on tropical forest restoration in a field-scale experiment. *Science. Advances*, 9, eadf0938.
- Zelnik, I. & Carni, A. (2013) Plant species diversity and composition of wet grasslands in relation to environmental factors. *Biodiversity and Conservation*, 22, 2179–2192.
- Zhang, C., Wang, J., Liu, W., Zhu, S., Ge, H., Chang, S.X. et al. (2010) Effects of plant diversity on microbial biomass and community metabolic profiles in a full-scale constructed wetland. *Ecological Engineering*, 36, 62–68.
- Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of Ecology*, 100, 742–749.
- Zhou, X., Zhang, M., Krause, S.M.B., Bu, X., Gu, X., Guo, Z. et al. (2021) Soil aeration rather than methanotrophic community drives methane uptake under drought in a subtropical forest. *Science of the Total Environment*, 792, 148292.
- Zhou, X., Zuo, H. & Smaill, S.J. (2021) Incorporation of NPP into forest CH₄ efflux models. *Trends in Plant Science*, 26, 1210–1212.
- Zomer, R.J., Trabucco, A., Bossio, D.A. & Verchot, L.V. (2008) Climate change mitigation: a spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems & Environment*, 126, 67–80.

SUPPORTING INFORMATION

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