

# Globally nitrogen deposition decreased net carbon sequestration in terrestrial ecosystems by increasing plant-derived carbon decomposition rather than soil priming effects: A meta-analysis

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## Research Article

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## Abstract

**Aims** Plant carbon (C) input and soil priming effects (PEs) together determine the net C sequestration of terrestrial ecosystems. These processes are recognized to be largely influenced by nitrogen (N) availability, the global patterns of N deposition effects on soil net C sequestration and the controlling factors for such effects remain unclear.

**Methods** In this study, we conducted a meta-analysis of 2205 observations from 56 studies worldwide to explore the effect of mineral N addition on net C sequestration and the associated drivers.

**Results** The meta-analysis found that although mineral N addition reduced soil PEs, it still decreased soil net C sequestration by increasing plant-derived C decomposition. The decrease of net C sequestration was much greater by urea addition than by ammoniacal and nitrate N addition. In addition, mineral N addition only decreased net C sequestration under pyrolytic C and residue C substrate forms. The higher soil organic C (SOC) and total N (TN) content increased net C sequestration by decreasing soil PEs rather than plant-derived C decomposition. Higher soil clay content reduced net C sequestration by increasing plant-derived C decomposition rather than soil PE. Higher incubation temperature reduced net C sequestration by increasing SOC and plant-derived C decomposition. Longer incubation time increased net C sequestration by reducing the decomposition of SOC and plant-derived C decomposition.

**Conclusions** These results are beneficial for understanding the response of soil net C sequestration to global N deposition, and could improve the prediction of terrestrial ecosystems C balance under global climate changes.

## Introduction

Soil carbon (C) pool is the largest C pool in terrestrial ecosystems (Bastida et al. 2019), and it is about 3 to 4 times of the vegetation C or atmospheric C pool (Jobbágy and Jackson 2000; Xu et al. 2013). A slight change in soil C storage under global climate changes will have a significant impact on carbon dioxide (CO<sub>2</sub>) emissions and global C cycle (Creamer et al. 2015; Fang et al. 2017). The soil C storage depends on the balance of the plant C input (such as rhizodeposition, straw returning and biochar amendment) and the loss through soil C decomposition (Dijkstra et al. 2021; Su and Shangguan 2023). The atmospheric nitrogen (N) deposition is predicted to increase the net primary production of terrestrial ecosystems (Stevens et al. 2015), thereby importing more plant C into the soil (Chen et al. 2022). Plant C input can promote the accumulation of soil organic C (SOC), but it also can alter the SOC decomposition through the soil priming effects (PEs), which thus alter the net C sequestration of terrestrial ecosystems (Fontaine et al. 2004; Maestrini et al. 2014; Zhang and Wang 2012).

Globally, many terrestrial ecosystems are experiencing an increase in anthropogenic derived N deposition (Chen et al. 2014; Galloway et al. 2008). A certain amount of N deposition is beneficial for increasing the terrestrial ecosystem productivity and promoting soil net C sequestration (Lu et al. 2021b; Song et al. 2020). However, excessive N deposition may cause adverse effects on terrestrial ecosystems (e.g., soil acidification, biodiversity loss and reduced crop yields), thereby inhibiting soil net C sequestration (Delgado-Baquerizo et al. 2018; Guo et al. 2010). An excessive N deposition tendency has been occurring on a global scale due to the excessive mineral N fertilizers application in agricultural production and the continuous burning of fossil fuels (Gruber and Galloway 2008; Wang et al. 2023). The global N deposition rates have exceeded 10–12 kg N ha<sup>-1</sup> yr<sup>-1</sup>, which is 5 to 20 times higher than the pre-industrial revolution and may increase more in the future (Cardinale et al. 2012; Kanakidou et al. 2016). Thus, it is important to investigate the effects of atmospheric N deposition (or artificial mineral N addition) on soil net C sequestration.

The N deposition or fertilization is often concurrent with plant C input in agricultural production (Wang et al. 2021; Zak et al. 2017). Some research has found that mineral N addition could significantly influence net C sequestration by changing plant-derived C and/or native SOC decomposition (Sun et al. 2022). Several theories have been proposed to explain these phenomena. The “co-metabolism hypothesis” states that the appropriate addition of plant C and mineral N can promote microbial metabolism and produce more extracellular enzymes (Blagodatskaya and Kuzyakov 2008; Li et al. 2021). However, these extracellular enzymes do not have selectivity (Burns et al. 2013; Sinsabaugh et al. 2008). Therefore, mineral N addition can decrease net C sequestration by synchronously increasing the PEs and plant-derived C decomposition. According to “microbial N mining hypothesis”, when soil is N-limited, microbes use plant C as energy to synthesize and secrete extracellular enzymes to decompose refractory soil organic matter to obtain N, thereby increasing the decomposition of plant C and native SOC (Craine et al. 2007; Moorhead and Sinsabaugh 2006). Thus, the addition of mineral N is beneficial to alleviate soil N limitation (Thomas et al. 2015; Zheng et al. 2022), and further reducing plant C and native SOC decomposition and increasing net C sequestration. The “stoichiometric decomposition hypothesis” suggests that when the C to N ratio (C/N) input matches microbial needs, the microbial activity is enhanced and the plant C and native SOC decomposition rates are higher (Cui et al. 2020; Wei et al. 2020). As the addition of mineral N can change the C/N of soil and exogenous additive (Hyvönen et al. 2008; Zhu et al. 2018), it will in turn change the plant-derived C decomposition, soil PEs and net C sequestration. The “preferential substrate utilization hypothesis”

illustrates that mineral N addition may change the preference of microorganisms from native SOC to plant-derived C (Blagodatskaya et al. 2007; Kuzyakov and Bol 2006), affecting the net C sequestration of terrestrial ecosystems. Hence the effect of mineral N addition on soil net C sequestration may be limited by multiple conditions, depriving the responses of net C sequestration to mineral N addition of universal mechanisms at a large scale.

Although numerous experimental studies on the effect of mineral N addition on soil net C sequestration have been conducted in cropland, forest and grassland, the results are contradictory. A recent study found that fungi assimilated a greater  $^{13}\text{C}$ -glucose proportion in the soil mixed with  $\text{NH}_4\text{Cl}$  and glucose than that with the sole glucose input, thereby alleviating N requirements of fungi, decreasing soil PEs and increasing net C sequestration (Su and Shangguan 2023). Compared with the sole glucose input, the mixed addition of  $\text{NH}_4\text{Cl}$  and higher glucose concentrations increased net C sequestration by 2.1 to 4.4%, while the mixed addition of  $\text{NH}_4\text{Cl}$  and lower glucose concentrations decreased net C sequestration by 2.4 to 3.0% (Zhu et al. 2022). However, another study found that there was no significant difference ( $P > 0.05$ ) in net soil C sequestration among the straw and N ( $\text{NH}_4\text{NO}_3$  or urea) mixed input treatments (Wang et al. 2018). The above contradictory results are likely resulted from the differences in soil characteristics (Sun et al. 2022; Zheng et al. 2023), ecosystem types (Guttières et al. 2021), plant C type (Bernal et al. 2016; Heitkötter et al. 2017), mineral N type (Li et al. 2017; Wang et al. 2018), exogenous C and N addition amounts (Auwal et al. 2021; Zheng et al. 2022). In addition, numerous traditional studies focused on the effect of mineral N addition on PEs, ignoring the its effect on plant-derived C decomposition (Feng and Zhu 2021). Many classical C and N cycle models also calculated plant C input and soil C output separately (Jenkinson and Coleman 2008; Manzoni and Porporato 2009). This brings great uncertainty to the prediction of global C and N cycle models, which limits the understanding of C cycles of terrestrial ecosystems on a global scale under the background of the N deposition. Thus, a meta-analysis is urgently needed to determine the responses of soil net C sequestration to mineral N addition on a global scale.

To fill these knowledge gaps, we used a global data set of 2205 paired observations from 56 publications that included 53 studies sites and 9 variables. The objectives of this study were to: (1) evaluate the responses of plant-derived C decomposition, soil PEs and net C sequestration to mineral N input; (2) explore how ecosystems type, plant C type, mineral N type and soil properties affect the responses across different studies.

## Methods

### Data sources and inclusion criteria

We searched peer-reviewed publications that were published before October 1, 2023, which investigated the effects of mineral N addition on plant-derived C decomposition, soil PEs and net C sequestration using the Web of Science and China National Knowledge. The search string was: (soil OR terrestrial OR land) and (nitrogen OR fertilization OR nutrient) and (addition OR input OR enrichment OR deposition OR application OR balance) and (mineralization OR decomposition OR respiration) and (isotope OR priming OR  $^{13}\text{C}$  labeled OR  $^{14}\text{C}$  labeled). The meta-analysis data met the following criteria: 1) the mineral N addition was set as the treatment group, while the without mineral N addition was treated as the control group; 2) the laboratory incubation experiments should be considered; 3) plant C input content should be reported; 4) plant C and mineral N should be added to the soil simultaneously; 5) plant-derived of  $\text{CO}_2\text{-C}$  and SOC-derived  $\text{CO}_2\text{-C}$  by  $^{13}\text{C}$  or  $^{14}\text{C}$  isotope tracer technique was reported; 6) to avoid the rhizosphere effect, experiments were conducted without roots. Totally, the meta-analysis included 2205 data of 56 articles (Fig. 1 and Table S1). The WebPlotDigitizer data extraction software was used to extract the data from the figure (Burda et al. 2017). If the standard deviation (SD) value of the publication was missed, we used 10% of the mean value as the SD value (Dong et al. 2022). If only standard error (SE) was reported in the publication, the following equation was used to estimate the SD value:  $\text{SD} = \text{SE} \times \sqrt{n}$ , where n represents the sample size. In addition, for categorical variables, mineral N type was grouped into ammoniacal nitrogen ( $\text{NH}_4^+$ ), nitrate nitrogen ( $\text{NO}_3^-$ ), and urea. Plant C type was grouped into root exudate C (such as glucose and oxalic acid), plant residue C (such as plant litter and residues), and pyrolytic C (such as biochar) (Luo et al. 2016; Reznik and Huttinger 2002; Yan et al. 2023). Soil ecosystems were grouped into cropland, grassland and forest.

### Data calculation and analyses

The plant-derived C decomposition ( $C_{\text{plant}}$ ), soil PEs ( $C_{\text{PE}}$ ) and net C sequestration were calculated as follows (Chen et al. 2022):

$$C_{\text{SOC}} = C_{\text{total}} \times (\delta_{\text{total}} - \delta_{\text{plant}}) / (\delta_{\text{without}} - \delta_{\text{plant}}) \quad (1)$$

$$C_{\text{plant}} = C_{\text{total}} - C_{\text{SOC}} \quad (2)$$

$$C_{\text{PE}} = C_{\text{SOC}} - C_{\text{without}} \quad (3)$$

$$\text{Net C sequestration} = E_p - (C_{\text{plant}} + C_{\text{PE}}) \quad (4)$$

The  $C_{\text{total}}$  is the total  $\text{CO}_2$  emissions of plant C input soil;  $C_{\text{SOC}}$  is the SOC-derived  $\text{CO}_2$ -C of plant C input soil;  $C_{\text{without}}$  is total  $\text{CO}_2$  emissions of without plant C input soil;  $E_p$  is C content of plant C input;  $\delta_{\text{total}}$  (‰) is the  $^{13}\delta$  of total  $\text{CO}_2$  respired from the plant C input soil;  $\delta_{\text{without}}$  (‰) is the  $^{13}\delta$  of total  $\text{CO}_2$  respired from the without plant C input soil;  $\delta_{\text{plant}}$  (‰) are the  $^{13}\delta$  of the plant C.

The variance ( $v$ ) and effect size (RR) were calculated in the following way (Dong et al. 2022; Feng and Zhu 2021):

$$RR = \frac{y_t - y_c}{\sqrt{\frac{(n_t-1)s_t^2 + (n_c-1)s_c^2}{n_t+n_c-2}}} \times \left(1 - \frac{3}{4(n_t + n_c - 2)}\right)$$

5

$$v = \frac{n_t + n_c}{n_t n_c} + \frac{RR^2}{2n_t + 2n_c}$$

6

The  $y_b$ ,  $s_t$  and  $n_t$  are the mean value, standard deviation (SD) and sample size of the mineral N input treatment group;  $y_c$ ,  $s_c$  and  $n_c$  are the mean value, SD and sample size of the control group.

Mean effect size ( $RR_{++}$ ) was calculated using the random-effects model (Li et al. 2018). We used the restricted maximum likelihood to calculate the between-study variance ( $\tau^2$ ). The  $\tau^2$  and within-study variance ( $v$ ) were used to calculate the weighting factor  $[1/(v + \tau^2)]$  (Dong et al. 2021). The variance-weighted bootstrapping method (999 iterations) was used to calculate the 95% confidence intervals (CI) (Liu et al. 2023). The weighted random forest model was used to analyze the relative variables importance (Zhang et al. 2023). The publication bias of research results was analyzed using trim-and-fill models and Rosenthal's fail-safe number (Table. S2). When the fail-safe number was greater than  $5n + 10$ , the study result was considered credible;  $n$  is studies original number (Yuan et al. 2021). When the RR recalculated by the models of trim-and-fill did not change significantly, it showed that the study result was also considered credible (Zhang et al. 2020). All data analyses in the research were performed using R (version 4.1.0) statistical software (Feng and Zhu 2021).

## Results

### Effects of mineral N type, plant C type and ecosystems

Mineral N addition generally increased plant-derived C decomposition ( $RR_{++}$ : 0.35, 95% CI from 0.25 to 0.46, Fig. 2a), while decreased soil PEs ( $RR_{++}$ : -0.79, 95% CI from -1.19 to -0.38, Fig. 2b) and net C sequestration ( $RR_{++}$ : -0.14, 95% CI from -0.23 to -0.06, Fig. 2c). Specifically,  $\text{NH}_4^+$  input increased plant-derived C decomposition ( $RR_{++}$ : 0.25, 95% CI from 0.09 to 0.47, Fig. 2a) and inhibited soil PEs ( $RR_{++}$ : -1.51, 95% CI from -2.12 to -0.91, Fig. 2b), thereby making no changes on soil net C sequestration ( $RR_{++}$ : 0.00, 95% CI from -0.12 to 0.12, Fig. 2c). The  $\text{NH}_4^+$  and  $\text{NO}_3^-$  mixed addition decreased soil net C sequestration ( $RR_{++}$ : -0.26, 95% CI from -0.40 to -0.13, Fig. 2c) by increasing plant-derived C decomposition ( $RR_{++}$ : 0.42, 95% CI from 0.25 to 0.58, Fig. 2a) rather than soil PEs ( $RR_{++}$ : -0.89, 95% CI from -1.52 to -0.26, Fig. 2b). However, urea input decreased soil net C sequestration ( $RR_{++}$ : -1.45, 95% CI from -1.73 to -1.18, Fig. 2c) by increasing plant-derived C decomposition ( $RR_{++}$ : 0.71, 95% CI from 0.47 to 0.96, Fig. 2a) and soil PEs ( $RR_{++}$ : 1.87, 95% CI from 0.95 to 2.80, Fig. 2b). Further, the  $RR_{++}$  of plant-derived C decomposition were 0.29 in exudate C addition soil (95% CI from 0.15 to 0.43), 0.31 in residue C addition soil (95% CI from 0.13 to 0.48) and 1.05 in pyrolytic C addition soil (95% CI from 0.66 to 1.45, Fig. 2a). The  $RR_{++}$  of soil PEs were -1.60 in exudate C addition soil (95% CI from -2.14 to -1.06), 0.02 in residue C addition soil (95% CI from -0.65 to 0.69) and 1.56 in pyrolytic C addition soil (95% CI from 0.06 to 3.07, Fig. 2b). The  $RR_{++}$  of net C sequestration were -0.06 in exudate C addition soil (95% CI from -0.18 to 0.05), -0.21 in residue C addition soil (95% CI from -0.34 to -0.07) and -0.30 in pyrolytic C addition soil (95% CI from -0.59 to -0.01, Fig. 2c).

The effects of mineral N addition on plant-derived C decomposition, soil PEs and net C sequestration varied with ecosystems. Mineral N addition increased plant-derived C decomposition ( $RR_{++}$ : 0.71, 95% CI from 0.47 to 0.96, Fig. 2a) and soil PEs ( $RR_{++}$ : 1.87, 95% CI from 0.95 to 2.80, Fig. 2b), and decreased soil net C sequestration ( $RR_{++}$ : -1.45, 95% CI from -1.73 to -1.18, Fig. 2c) in grassland soil. For forest soil, mineral N addition increased plant-derived C decomposition ( $RR_{++}$ : 0.58, 95% CI from 0.42 to 0.75, Fig. 2a) and inhibited soil PEs ( $RR_{++}$ : -2.50, 95% CI from -3.12 to -1.87, Fig. 2b), thereby making no changes on soil net C sequestration ( $RR_{++}$ : 0.04, 95% CI from -0.12 to 0.19,

Fig. 2c). However, the input of mineral N did not affect plant-derived C decomposition ( $RR_{++}$ : 0.00, 95% CI from -0.15 to 0.16, Fig. 2a), soil PEs ( $RR_{++}$ : -0.33, 95% CI from -0.91 to 0.26, Fig. 2b) and soil net C sequestration ( $RR_{++}$ : 0.00, 95% CI from -0.15 to 0.15, Fig. 2c) of cropland soil.

#### Factors influencing the effect size of mineral N addition

The RR of mineral N on plant-derived C decomposition was positively correlated with SOC, total nitrogen (TN), soil clay content, exogenous additives C/N, and incubation temperature, but was negatively correlated with incubation time (Fig. 3). The RR of mineral N on soil PEs was positively correlated with soil C/N, soil pH and incubation time, while was negatively correlated with SOC, TN, soil clay content, exogenous additives C/N, and incubation time (Fig. 3). The RR of mineral N on net C sequestration was positively correlated with SOC, TN, and incubation time, while was negatively correlated with soil C/N, soil clay content, and incubation temperature (Fig. 3). The weighted random-forest model further found that exogenous additives C/N was the most important factor mediating the effects of mineral N addition on plant-derived C decomposition and soil PEs, and soil C/N was the most important factor mediating the effect of mineral N addition on net C sequestration (Fig. 4).

## Discussion

### Mineral N addition decreased net C sequestration

The study found that although mineral N addition inhibited soil PEs ( $RR_{++}$ : -0.79), and it reduced soil net C sequestration ( $RR_{++}$ : -0.14) by increasing plant-derived C decomposition ( $RR_{++}$ : 0.35, Fig. 2). Previous studies also found that the mineral N addition reduced soil PEs and increased litter decomposition rate (Feng and Zhu 2021; Wu et al. 2023), which was consistent with the present view. According to the “preferential substrate utilization hypothesis”, the preferential uptake of C-rich and N-rich exogenous substrates by soil microorganisms is likely a potential mechanism of the negative effect on net C sequestration (Kuzyakov and Bol 2006). The mixed input of plant C and mineral N meets the microbial demand for C and N, converting slow-growing K-strategists microorganisms from SOC decomposition to plant C uptake (Blagodatskaya et al. 2007; Su and Shangguan 2023). This would result in the negative effect on net C sequestration. Compared with other mineral N types, urea addition decreased soil net C sequestration by increasing plant-derived C decomposition and soil PEs (Fig. 2). As urea cannot be directly absorbed by microorganisms, they need to secrete a large amount of extracellular enzymes (e.g., urease and extracellular depolymerases) to convert urea into small organic molecules, such as  $NH_4^+$  and  $NO_3^-$  (Geisseler et al. 2010; Li et al. 2017; Wang et al. 2018). However, these extracellular enzymes do not have selectivity (Burns et al. 2013; Sinsabaugh et al. 2008), which may simultaneously increase SOC and plant-derived C decomposition, thereby reducing net C sequestration.

The effects of mineral N addition on net C sequestration were also dependent on plant C types. Pyrolytic C input decreased soil net C sequestration by increasing plant-derived C decomposition and soil PEs (Fig. 2). The nutrient content and stoichiometry characteristics of plant C may have important effects on the decomposition of SOC and plant C (Wang et al. 2014). Compared with exudate C and residue C, pyrolytic C has higher C content (Fig. S1). Therefore, only pyrolytic C input in the short term may lead to extreme stoichiometric imbalance (high C/N) in soil (Rasul et al. 2022), thereby reducing the decomposition of SOC and pyrolytic C (Clough and Condron 2010; Sun et al. 2019). In addition, pyrolytic C has a large specific surface area and highly porous structure, so it has a strong adsorption potential (Fang et al. 2015; Jiang et al. 2016). The mineral N in the soil solution are more easily fixed in the pyrolytic C pores through electrostatic adsorption, ion exchange and complexation reaction (Clough et al. 2013), thereby reducing the accessibility of soil microorganisms to mineral N in soil (Gul and Whalen 2016). However, the addition of mineral N can increase the soil N concentration and reduce the soil C/N (Zheng et al. 2022), which is beneficial for the utilization of plant C and SOC by microorganisms, thereby reducing soil net C sequestration.

For different types of ecosystems, mineral N addition increased plant-derived C decomposition and inhibited soil PEs, thereby making no changes in net C sequestration of forest soil (Fig. 2). However, mineral N addition decreased soil net C sequestration in grasslands by increasing plant-derived C decomposition and soil PEs (Fig. 2). Previous studies have found that mineral N addition reduced the oxidative enzyme activity in forest ecosystems and increased the oxidative enzyme activity in grassland ecosystems (Riggs and Hobbie 2016; Xiao et al. 2018). Because the basidiomycete is dominant in forest soil, mineral N addition often leads to the loss of oxidative enzyme activity, while ascomycota and ascomycota are dominant in grassland soil, which is conducive to the protection of oxidative enzyme activity (Sinsabaugh 2010). Higher oxidative enzyme activity increased the decomposition of plant C and SOC by grassland soil microorganisms (Duan et al. 2021; Luo et al. 2020), thereby reducing soil net C sequestration.

### Driving factors of net C sequestration by mineral N addition

The effect of mineral N addition on soil net C sequestration was closely related to soil properties. The study showed that soil net C sequestration with N addition was positively related to SOC and TN contents, which was likely resulted from soil PEs inhibition (Fig. 3a, b). Compared with the fertile soil, the poor soil is usually dominated by starvation-tolerant microbial communities, which may induce greater soil PEs upon receiving plant C and mineral N mixed addition (Conant et al. 2011; Dong et al. 2022; Holden and Fierer 2005). The higher C/N decreased net C sequestration by increasing soil PEs (Fig. 3c). As we know that mineral N addition can reduce soil C/N. According to the “stoichiometric decomposition hypothesis”, lower soil C/N is beneficial to meet soil microbial demand for C and N sources (Ehtesham and Bengtson 2017), thereby promoting soil PEs. In addition, higher soil clay content decreased net C sequestration by increasing plant-derived C decomposition (Fig. 3e). Possibly, the higher soil clay content is conducive to the physical protection of soil aggregates and the accumulation of nutrients (Angst et al. 2021; Lu et al. 2021a). At the same time, the addition of mineral N was beneficial to the C occlusion in soil aggregation with higher clay content, which reduces the availability of SOC by microorganisms (Riggs et al. 2015). In contrast, microorganisms may have more access to plant-derived C (Blagodatskaya et al. 2007; Kuzyakov and Bol 2006), resulting in an increased plant-derived C decomposition under higher soil clay content. Meanwhile, the higher incubation temperature increased SOC and plant-derived C decomposition and decreased net C sequestration (Fig. 3g). The fast growth of soil microorganisms at higher temperature could lead to more soil N immobilization, thus decreasing N availability (Dong et al. 2022; Wang et al. 2021). The mineral N input can supplement the soil N loss caused by microorganism growth (Geisseler et al. 2010; Wang et al. 2021), thus further promoting the assimilation of SOC and plant C by microorganisms. Finally, the study found that plant-derived C decomposition and soil PEs were negatively correlated with soil incubation time, while net C sequestration was positively correlated with soil incubation time (Fig. 3h). Some previous studies have found that mineral N addition increased the stabilization of plant C and SOC in humus by promoting hydrophobic protection (Luo et al. 2019; Spaccini et al. 2002). With the increase of incubation time, the accumulation of soil humus can protect plant C and SOC from microbial decomposition, thus increasing soil C sequestration (Giesler et al. 2004; He et al. 2023; Kleber et al. 2015).

## Conclusion

By integrating pairwise data from multiple studies, we have generalized the effect of mineral N addition on soil net C sequestration on a global scale. The mineral N addition decreased soil net C sequestration ( $RR_{++}$ : -0.14) by increasing plant-derived C decomposition ( $RR_{++}$ : 0.35) rather than soil PEs ( $RR_{++}$ : -0.79). The effects of mineral N addition varied with soil characteristics, ecosystem types, plant C type, mineral N type, incubation time and temperature. The effect size of urea addition ( $RR_{++}$ : -1.45) on soil net C sequestration was greater than ammonium and nitrate N mixed addition ( $RR_{++}$ : -0.26). The effect sizes of mineral N on soil net C sequestration were positively correlated with SOC, TN and incubation time, while negatively correlated with soil C/N, clay content and incubation temperature. In a word, this study revealed that although mineral N addition reduced the soil PEs, it could decrease soil net C sequestration by increasing plant-derived C decomposition. These findings improve the understanding of the effects of plant C input and SOC decomposition on soil net C balance under global N deposition conditions and are helpful for more accurately predicting regional and/or global C budgets in terrestrial ecosystems.

## Abbreviations

C	Carbon
SOC	Soil organic carbon
CO <sub>2</sub>	Carbon dioxide
N	Nitrogen
TN	Soil total nitrogen
NH <sub>4</sub> <sup>+</sup>	Soil ammoniacal nitrogen
NO <sub>3</sub> <sup>-</sup>	Soil nitrate nitrogen
C/N	C to N ratio
PEs	Priming effects
CI	Confidence interval
RR	Effect size (or Response ratio)
SE	Standard error
SD	Standard deviation
Exudate C	Root exudate carbon
Residue C	Plant residue carbon
Pyrolytic C	Pyrolytic carbon
Q <sub>M</sub>	Difference in group cumulative effect sizes
Q <sub>E</sub>	Residual errors

## Declarations

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## Tables

Table 1

Relationships between the effect size of plant-derived carbon (C) decomposition, soil priming effects and net C sequestration with measured variables. n: data points number. Time, soil incubation time; Temperature, soil incubation temperature.

Variables	Plant-derived C decomposition				Soil priming effects				Net C sequestration			
	n	Q <sub>E</sub>	Q <sub>M</sub>	P	n	Q <sub>E</sub>	Q <sub>M</sub>	P	n	Q <sub>E</sub>	Q <sub>M</sub>	P
Exogenous C/N	691	1895	100.67	0.000	691	5123	12.29	0.001	691	2405	0.21	0.648
Time (day)	735	2037	19.32	0.000	735	5453	6.10	0.014	735	2389	14.42	0.000
Temperature (°C)	711	2053	4.10	0.043	711	5438	13.85	0.000	711	2377	11.30	0.001
Depth (cm)	700	1925	0.21	0.650	700	5215	0.20	0.634	700	2359	2.67	0.102
SOC (%)	613	1912	15.18	0.000	613	4783	10.02	0.002	613	2286	15.65	0.000
TN (%)	585	1771	14.02	0.000	585	4421	21.44	0.000	585	2053	21.35	0.000
C/N	603	1806	2.83	0.093	603	4524	5.92	0.009	603	2129	38.32	0.000
pH	650	1790	1.25	0.264	650	4871	4.30	0.038	650	2130	0.88	0.878
Clay (%)	367	1061	17.57	0.000	367	2611	4.72	0.030	367	835	12.16	0.001

Figures

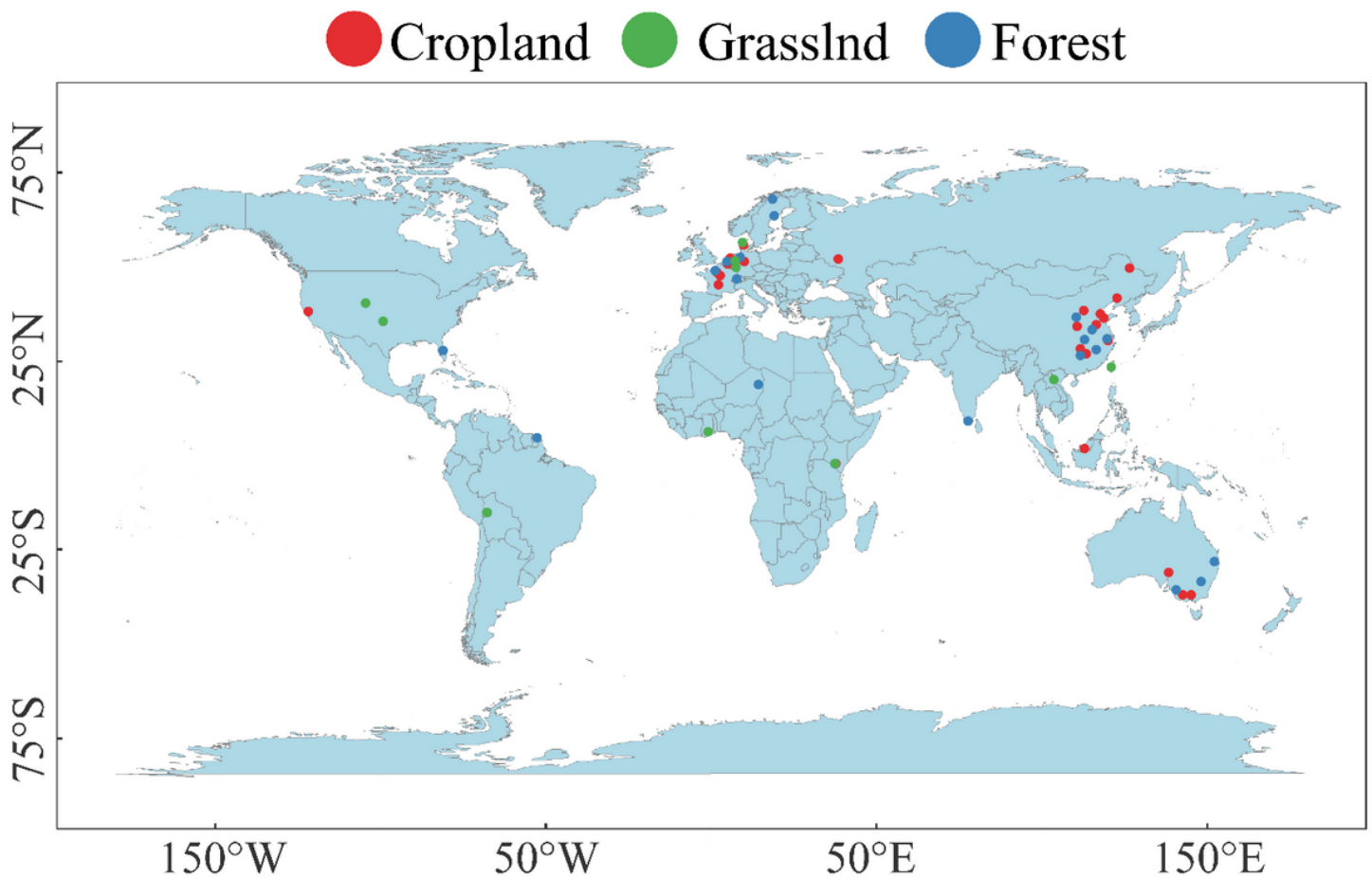
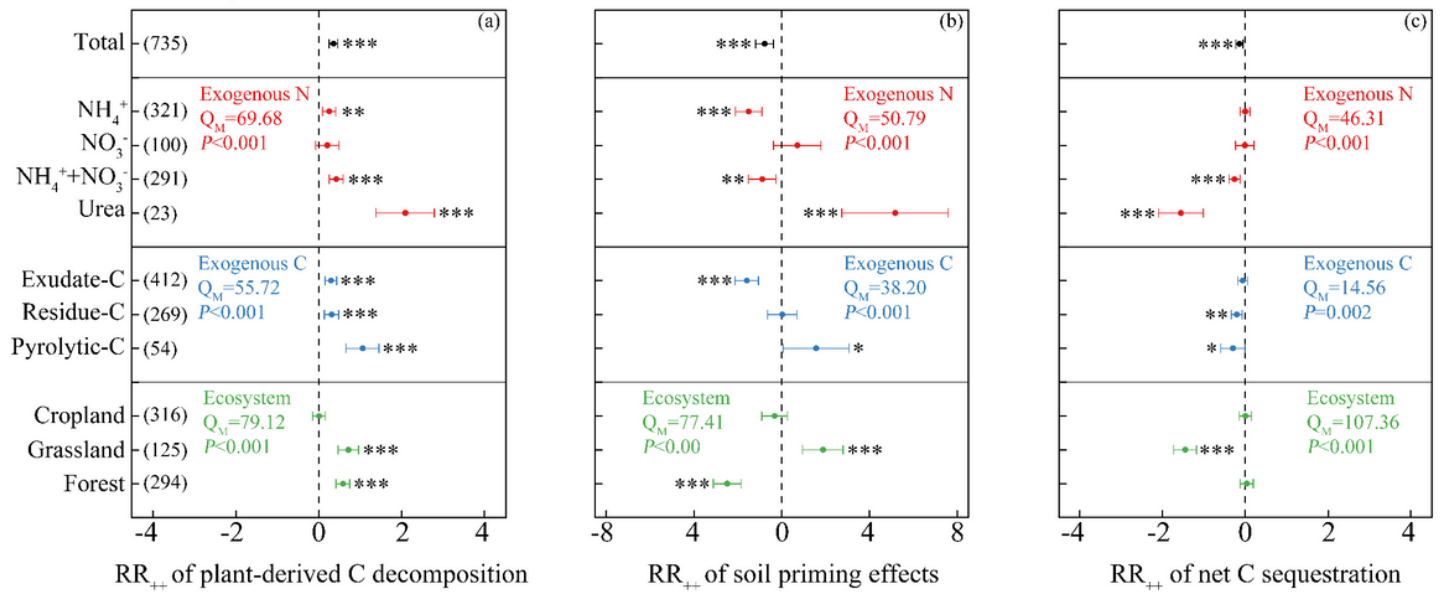


Figure 1

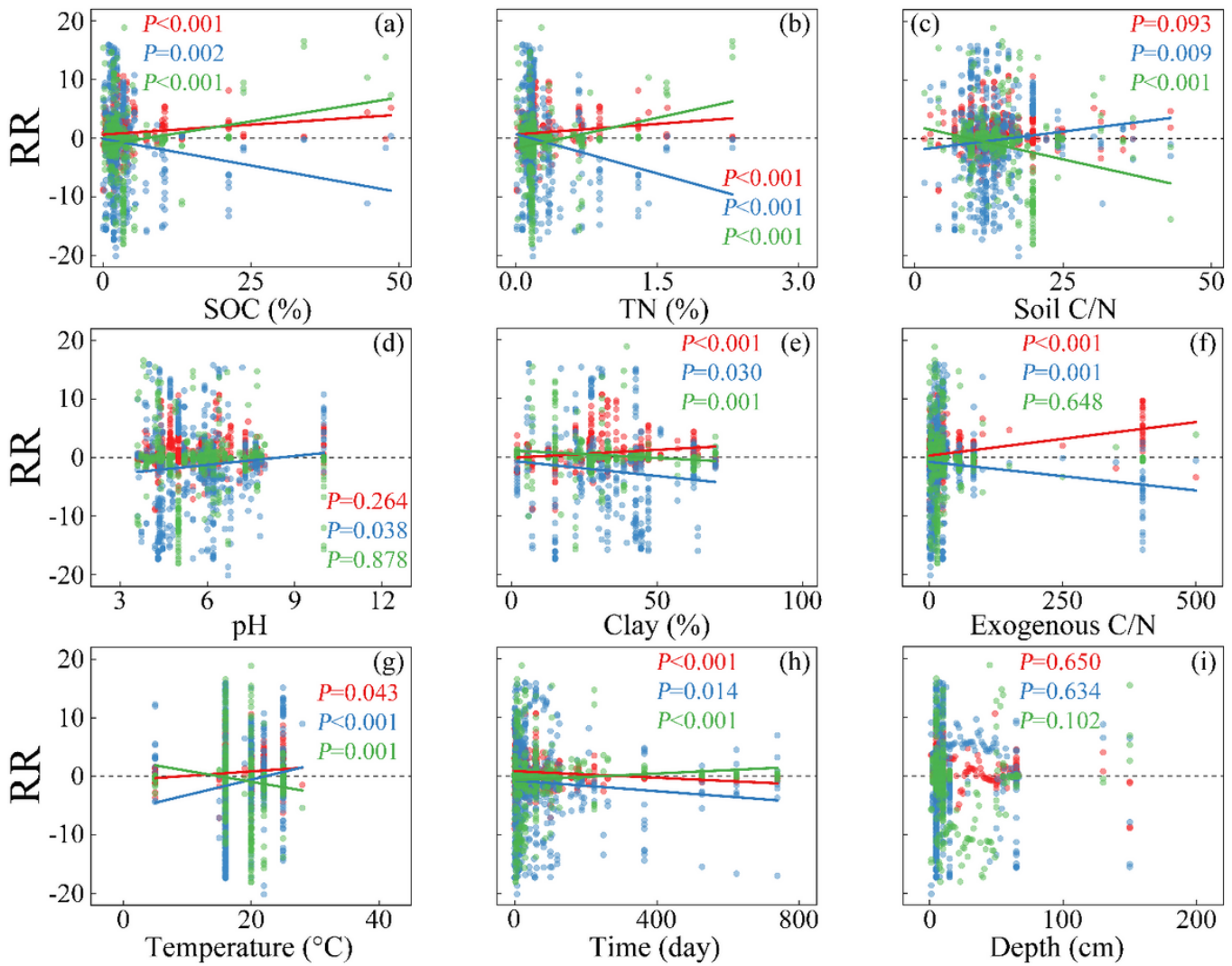
Global distribution of locations of studies included in this study.



**Figure 2**

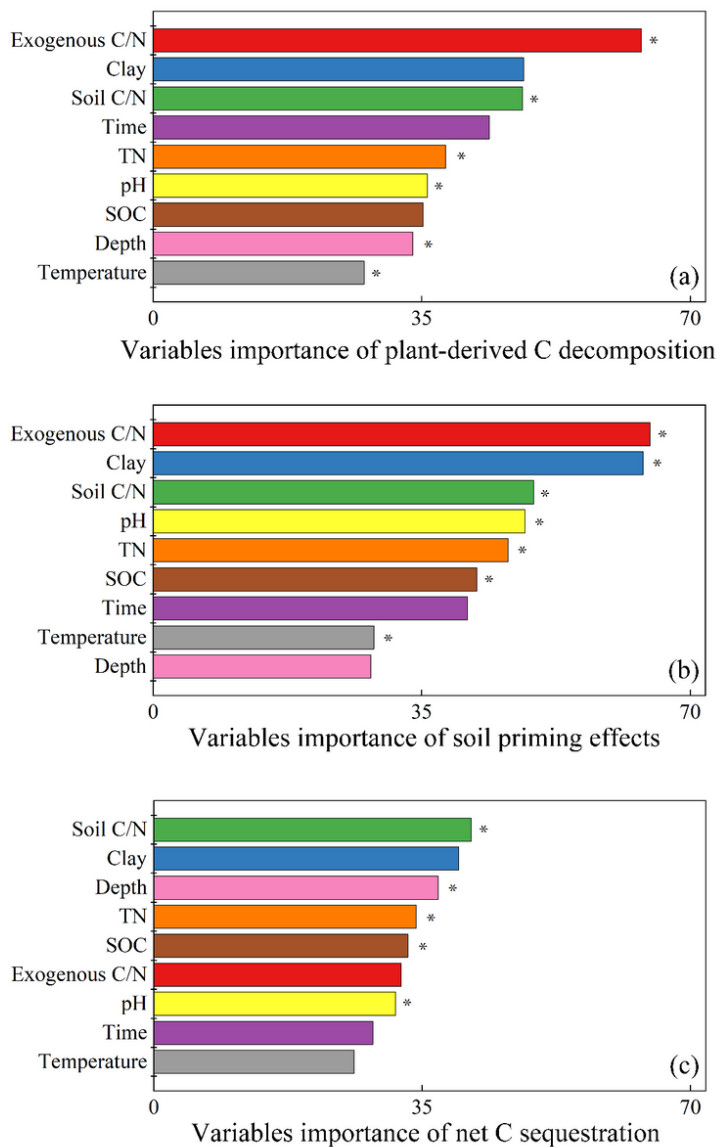
Comparisons of the plant-derived carbon (C) decomposition, soil priming effects and net C sequestration mean effect size (RR<sub>++</sub>) to nitrogen (N) input among different exogenous N type, different exogenous C type and different ecosystem types. Error bars represent 95% bootstrapped CIs. If the 95% CIs did not overlap with the zero line, the effect of the study was considered significant (\*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001).

— Plant-derived C decomposition — Soil priming effects — Net C sequestration



**Figure 3**

The linear relationships between the effect size (RR) of plant-derived carbon (C) decomposition, soil priming effects and net C sequestration with measured variables. Time, soil incubation time; Temperature, soil incubation temperature.



**Figure 4**

Variable's importance of moderators for the effect of plant-derived carbon (C) decomposition, soil priming effect and net C sequestration by a random forest model. If the  $P < 0.05$ , we use the asterisks (\*) to indicate significant moderators. Time, soil incubation time; Temperature, soil incubation temperature.

## Supplementary Files

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