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RESEARCH ARTICLE

Decrease in soil pH has greater effects than increase in above-ground carbon inputs on soil organic carbon in terrestrial ecosystems of China under nitrogen enrichment

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Abstract

1. Impacts of nitrogen (N) enrichment on soil carbon (C) budgets in terrestrial ecosystems have been well documented by numerous field experiments and syntheses. Although previous studies have largely attributed this phenomenon to the increased organic C inputs, the potential mechanisms of how N enrichment increases soil organic C (SOC) remain contentious.
2. In this study, we conducted a meta-analysis comprising 234 published field N-addition experiments from multiple terrestrial ecosystems across China to evaluate the impacts of N enrichment on the SOC budget.
3. Although the meta-analysis revealed that N-addition significantly enhanced plant biomass and SOC concentration across the selected studies, we found that SOC concentration was independent of, or even decreased with, the enhanced plant biomass due to increased soil C loss as increasing organic C inputs. The negative correlation between plant C inputs and SOC under N enrichment, meanwhile, appeared reversible by the concomitant changes in soil pH, which depended on the magnitude of soil acidification. Increased SOC in terrestrial ecosystems was closely associated with decreased soil pH, which reduced soil C losses by limiting microbial degradation.
4. *Synthesis and applications*. We suggest that soil carbon (C) budget is determined by the trade-off between plant C inputs and nitrogen (N)-induced soil acidification. In contrast to other studies, our findings demonstrate that N-mediated soil acidification, rather than increased above-ground C inputs, is the main driver increasing soil organic C (SOC) under elevated N inputs in terrestrial ecosystems of China.

KEYWORDS
carbon cycling, meta-analysis, nitrogen addition, soil acidity, soil organic carbon, terrestrial ecosystems

1 | INTRODUCTION

Despite the global success of environmental legislation that has resulted in decreases in emissions of nitrogen (N) compounds to the atmosphere in many regions (Gilliam et al., 2019; Schmitz et al., 2019), N emissions continue to rise in other regions from chronic expansion of industry, agriculture and animal husbandry (Galloway et al., 2004, 2008). Global annual N deposition has increased more than fivefold compared with 100 years ago, a rate exceeding natural biological N fixation (Lamarque et al., 2005). Elevated N deposition greatly influences the carbon (C) cycle in terrestrial ecosystems regionally and globally (Chuman et al., 2021; Ma et al., 2021; Song et al., 2019). Although numerous field experiments (e.g. Averill & Waring, 2018; Geng et al., 2021; Lu, Guo & Hou, 2021; Lu, Vitousek, et al., 2021) and syntheses (e.g. Deng et al., 2018; Xu et al., 2021) have demonstrated that N enrichment can promote an accumulation of soil organic C (SOC), the underlying mechanisms for this remain unclear, resulting in a wide debate about the interrelationships between plant and soil C dynamics under N enrichment (Liu & Greaver, 2010; Xu et al., 2021; Ye et al., 2018).

Nitrogen enrichment enhances plant production via increasing N availability and stimulating photosynthetic capacity, thereby increasing plant C fixation (Liang et al., 2020; Zhang, Li, et al., 2018). Nitrogen addition significantly increased plant biomass and litterfall globally (Li et al., 2020; Schulte-Uebbing & de Vries, 2018), which was considered to be the main driver of increases in soil C accumulation (LeBauer & Treseder, 2008; Zhao et al., 2018). These conclusions are typically based on calculations showing that large amounts of C fixed annually by plants are sequestered in below-ground pools. Mounting evidence, however, finds that the soil C storage does not always mirror the above-ground C inputs (Liu & Greaver, 2010; Lu, Guo, et al., 2021; Lu, Hou, et al., 2021; Song et al., 2019). Kuzyakov et al. (2000) proposed a priming effects model suggesting that enhancement of above-ground organic matter inputs from N enrichment may increase soil C loss due to the changes in plant tissue chemistry. For instance, exogenous N inputs altered the quality of litter by reducing foliar C:N ratios and decreasing lignin concentrations (Sun et al., 2020), resulting in faster rates of litter decomposition. According to the priming effect hypothesis, the increase in N availability and labile C substrates promotes microbial C utilization, thereby increasing the degradation of recalcitrant organic matter and leading to a negative effect on soil C accumulation over the long term (Riggs & Hobbie, 2016).

Theoretically, if N enrichment-enhanced soil C storage is determined by plant inputs, then N fertilization should promote microbial decomposition of native SOC, decreasing soil C concentration (Cheng et al., 2014; Kuzyakov et al., 2000). Numerous studies, in fact, have reported that N enrichment could inhibit organic C decomposition and microbial C utilization, even when N-addition accompanies enhancement of substantial quantities of labile organic matter inputs (Jia et al., 2020; van Diepen et al., 2015; Zhang et al., 2018). Moreover, a previous study reported that SOC can be altered by N-addition even when organic matter inputs do not change (Janssens et al., 2010), suggesting the existence of a non-plant-derived mechanism for enhanced soil C stocks. Still other work has demonstrated N-mediated alterations in soil microbial communities and associated reductions in oxidative enzymes, further inhibiting decomposition (e.g. Carrara et al., 2018; Moore et al., 2021). These results suggest that soil C accumulation under N enrichment is not regulated simply by the quantity or the quality of organic matter inputs.

Although most studies to date have attributed SOC accumulation to biotic factors (litter inputs and microbial decomposition), recent studies have found that the influence of N-addition on SOC was frequently linked to an abiotic factor, that is, N-induced soil acidification (Averill & Waring, 2018; Bonner et al., 2019; Zhang et al., 2020). Multiple hypotheses have been proposed to link shifts in soil pH with the alteration of SOC under N enrichment. For instance, the acidity hypothesis proposed that microbial biomass and decomposition rates of organic matter increase when micro-organisms are released from N limitation under N enrichment, but increased N availability may also mask these positive effects on soil micro-organisms, since concomitant declines in soil pH values inhibit microbial activity (Averill & Waring, 2018). In addition, soil acidification could affect the stability of SOC by changing pH-sensitive associations between organo-minerals and organic C (Lu, Guo, et al., 2021; Lu, Hou, et al., 2021; Ye et al., 2018). This physical protection mechanism can strongly inhibit soil microbial C utilization. Accordingly, N enrichment may regulate SOC accumulation primarily by reducing soil C loss via decreasing soil pH rather than by increasing organic C inputs.

Because of the rapid economic development, annual N deposition in China has increased more than 60% since the 1980s (Liu et al., 2013), resulting in an average decline of soil pH by 0.5 units in cropland across China (Guo et al., 2010). The complex spatial variations and multiple land-use types in China provide a suitable reference for assessing the effects of N enrichment on soil C dynamics regionally and globally. The purpose of this study was to synthesize available data from field experiments in China and to evaluate the general effect of N-enrichment-induced soil acidification on SOC accumulation. In addition, we addressed the potential mechanisms of regulation by variation of soil acidity on soil C accumulation in terrestrial ecosystems.

2 | MATERIALS AND METHODS

2.1 | Variable selection and data collection

To assess N-mediated changes in soil C-related processes (i.e. plant C inputs and soil C losses), we performed a meta-analysis of studies documenting the impacts of N-addition on plant, soil and microbial C-related variables. We used the Web of Science (WoS, before December 2020) to select peer-reviewed publications reporting effects of N-addition on C-related variables, and changes in soil pH. The search terms were selected based on similar meta-analysis (Lu, Guo, et al., 2021; Lu, Hou, et al., 2021; Xu et al., 2021), and the keywords selected for online searching were '(nitrogen deposition OR nitrogen addition OR nitrogen enrichment OR nitrogen application OR nitrogen fertilization) and (soil organic carbon OR dissolved organic carbon OR microbial biomass carbon OR aboveground biomass OR litter OR root OR respiration OR microbe OR extracellular enzyme OR pH)'.

To avoid potential selection bias, we used the following criteria for data collection: (a) the studies reported the results of field N-addition experiments, with the exclusion of open-top container experiments and laboratory incubation studies. (b) Experiments had both control and treatment groups under the same geographical conditions, and each group has at least three replicates. (c) Means, standard deviations/errors, and sample size in the control and treatment groups could be collected from tables, or could be extracted by Engauge Digitizer (http://markummitchell.github.io/engauge-digitizer) and (d) different fertilization levels were collected as independent observations in one study. If the same study included multiple measurements at different sampling times or soil depths, only the latest and surface soil measurements were extracted. Finally, a total of 2,022 pairs of observations across the major terrestrial ecosystems of China in 234 peer-reviewed publications were collected (Figure 1). The selection procedure is illustrated in a PRISMA flow diagram (see Figure S1).

2.2 | Data compilation

The dataset contained 19 numerical variables classified into four groups: (a) plant C-related variables (i.e. above-ground biomass, litter mass, litter C:N ratio, root biomass, fine root biomass and fine root C:N ratio); (b) soil C-related variables (i.e. soil organic C, dissolved organic C, microbial biomass C, soil respiration, heterotrophic respiration and autotrophic respiration); (c) soil microbial C-related variables (i.e. total phospholipid fatty acids, bacterial biomass, fungal biomass, β-glucosidase activity, peroxidase activity and polyphenol oxidase activity) and (d) soil pH. We assessed the general influence of N-addition on above-ground C inputs, below-ground C accumulation and soil C loss via the changes in plant, soil and microbial C variables.

Ecosystem type, fertilization rate and experimental duration of each extracted observation were collected as moderator variables. To determine whether the response of soil C-related processes to N enrichment was dependent on ecosystem types or fertilization regimes, all data were divided into three subgroups according to ecosystem type (natural forest, grassland, plantation or cropland), experimental N-addition level (low [≤50 kg N ha^{-1} $year^{-1}$], medium [51 − 100 kg N ha^{-1} $year^{-1}$] or high [>100 kg N ha^{-1} $year^{-1}$]) and experimental duration (≤5, 6–10 or ≥11 year). The thresholds were those used in other meta-analyses (Song et al., 2019; Xu et al., 2021). In addition, we calculated the difference in soil pH (ΔpH) between the N-addition treatment and the control, and then divided the difference into three levels based on the average soil pH decline value (0.5 unit) across China (Guo et al., 2010) (i.e. non-acidified [≥0], mildly acidified [−0.5 to 0] and severely acidified [<−0.5]). Additional information on environmental variables of the experimental plots (i.e. latitude and longitude, mean annual temperature [MAT], and mean annual precipitation [MAP]) were also collected at the same time.

2.3 | Statistical analysis

The effect size and its variance were calculated according to a meta-analyses method by Hedges et al. (1999). The ln-transformed response ratio (lnRR) was used to evaluate how variables responded to N enrichment:

$$\ln(RR) = \ln\left(\overline{X}_t/\overline{X}_c\right) = \ln\left(\overline{X}_t\right) - \ln\left(\overline{X}_c\right),$$

where $\overline{X}_t$ and $\overline{X}_c$ represent the mean values of the treatment and the control groups, respectively. The variance (v) was calculated as follows:

$$v = \frac{S_t^2}{n_t\overline{X}_t^2} + \frac{S_c^2}{n_c\overline{X}_c^2},$$

where S_t and S_c represent the standard deviations of the treatment and control groups, respectively, and n_t and n_c are the sample sizes.

The 'METAFOR' package (version 2.4, Viechtbauer, 2010) in R software (version 4.1.0, R Development Core Team, 2019) was used to calculate the weighted response ratio ($\ln RR_+$) and to implement moderator variables (e.g. ecosystem type) with inverse-variance-weighted regressions and random-effects models. To handle the non-independence of within-paper data (multiple observations collected from one study), a two-step method was performed (Song et al., 2020), that is, first calculated the weighted response ratio about multiple observed response ratio in one study, and then access the overall response ratio by a standard random-effect method, with each 'study' as random factor. The responses of C-related variables to N-addition were considered to be significant if the 95% confidence intervals (CIs) did not overlap zero. Finally, we transformed $\ln RR_+$ to the percentage change to further evaluate the impacts of N on the selected variables:

$$\text{Effect size}(\%) = \left(e^{\ln RR_+} - 1\right) \times 100\%.$$

To determine whether the responses of each variable differed among ecosystem types or fertilization regimes, we partitioned total heterogeneity (Q_t) in each category into within-group (Q_w) and between-group (Q_b) heterogeneity. To determine the potential mechanisms of N-enrichment regulation on soil C accumulation, we used a single meta-regression model to examine the relationship between the response ratio of C-related variables. In addition, publication bias was evaluated by funnel plots using the 'funnel' function (Figure S6). A 'leave-one-out' test was conducted to examine

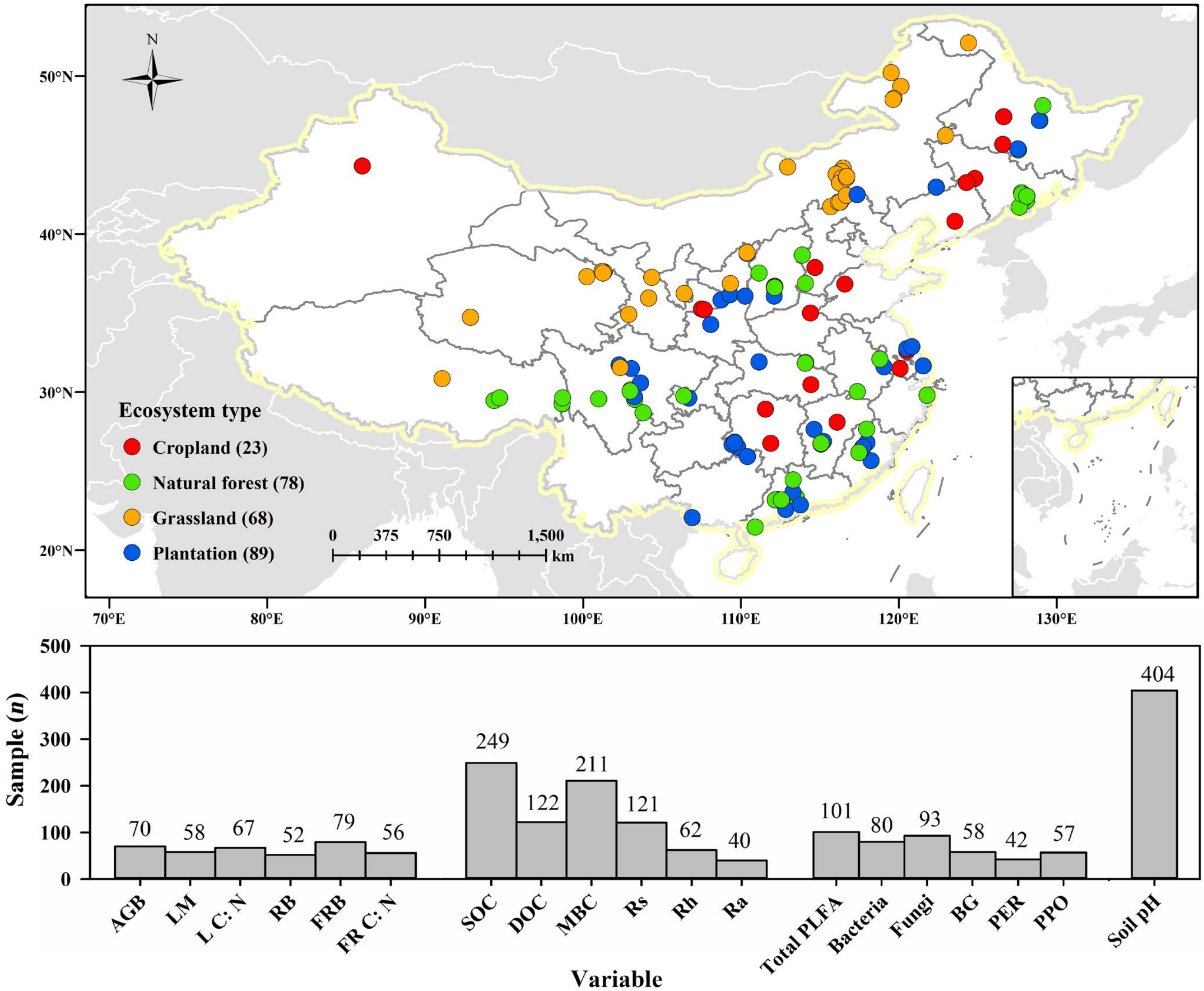

FIGURE 1 Geographical distribution of N-addition experiments included in this meta-analysis (top panel), and numbers of samples for the indicated variables (bottom panel). Abbreviations: AGB, above-ground biomass; BG, β-glucosidase activity; DOC, dissolved organic C; FR. C:N, fine root C:N ratio; FRB, fine root biomass; L. C:N, litter C:N ratio; LM, litter mass; MBC, microbial biomass C; PER, peroxidase activity; PPO, polyphenol oxidase activity; Ra, autotrophic respiration; RB, root biomass; Rh, heterotrophic respiration; Rs, soil respiration; SOC, soil organic C

the robustness of the response ratio via the 'leave1out' function (Figure S7). Significance was set at $p < 0.05$.

3 | RESULTS

3.1 | Effect of N-addition on soil C budget

Except for fine root biomass, all plant C-related variables were significantly affected by N-addition (Figure 2a). Nitrogen addition significantly increased above-ground biomass, litter mass and root biomass by 44%, 18% and 13%, respectively, and litter and fine roots C:N ratios decreased on average by 16% and 10%, respectively. For soil C pool, N-addition significantly increased SOC concentration by 5%, but decreased microbial biomass C (MBC) concentration by 7% (Figure 2b). Total soil respiration, as well as heterotrophic/autotrophic respiration, was not significantly affected by N-addition. On average, N-addition had minor effects on soil microbial biomass and extracellular enzyme activities (Figure 2c). Only the activity of peroxidase was significantly decreased (by 15%) under N fertilization. Detailed information for the effects of the ecosystem and fertilization regime on C-related variables is presented in Table S1 and Figures S2–S4.

3.2 | Effect of N-addition on soil acidification

On average, soil pH decreased significantly by 6% (0.37 units) by N fertilization relative to the controls (Figure 3). Although N enrichment tended to reduce soil pH in all cases, the effects of N-addition

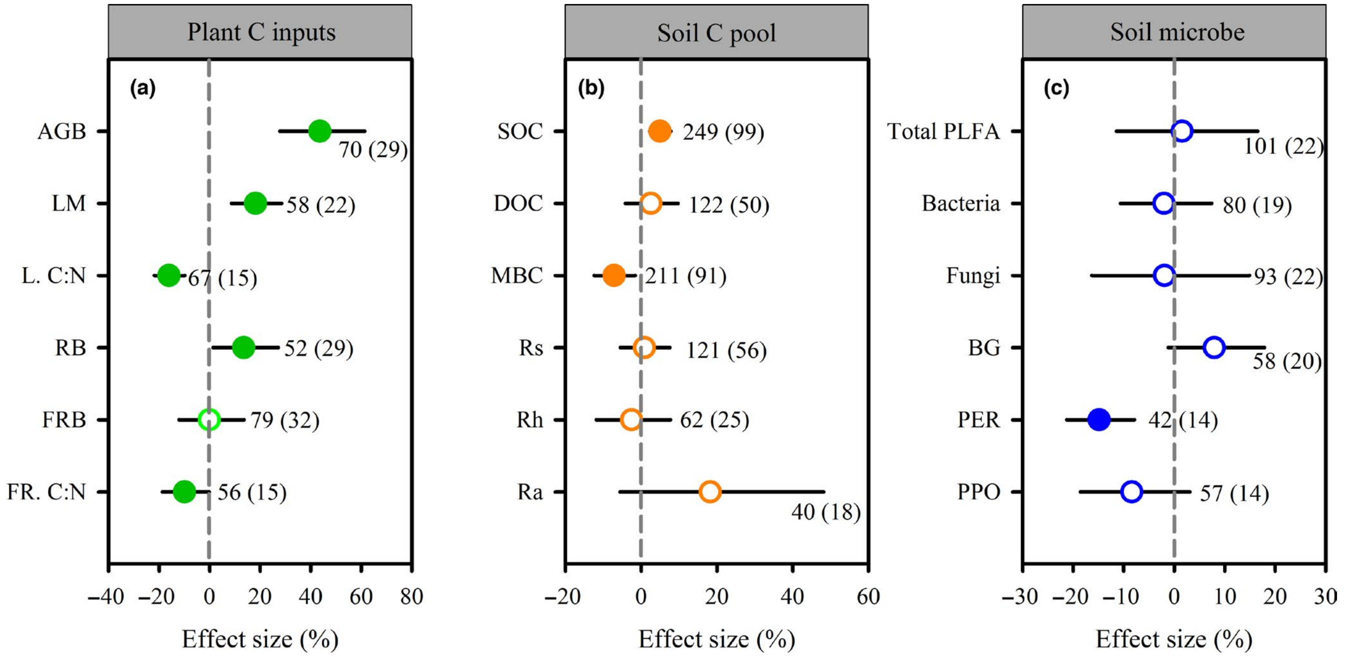

FIGURE 2 Effects of N-addition on plant (a), soil (b) and microbial (c) C-related variables. Dots represent effect sizes with 95% confidence intervals (CIs). Values adjacent to the bars indicate numbers of observations and studies (in brackets). Closed and open circles represent significant effects and insignificant effects, respectively. See Figure 1 for abbreviations

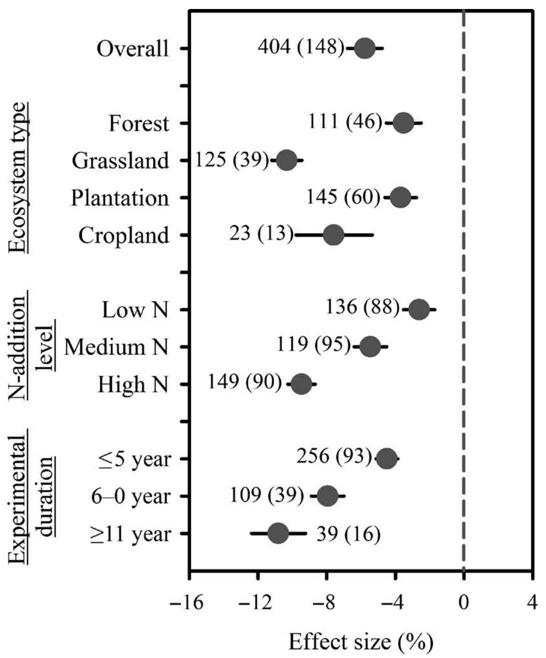

FIGURE 3 Effects of N-addition on soil pH as related to ecosystem type, N-addition level and experimental duration. Dots represent effect sizes with 95% confidence intervals (CIs). Values adjacent to the bars are numbers of observations and studies (in brackets)

on soil pH differed among ecosystem types and fertilization regimes ($p < 0.01$). Among the ecosystems, soil acidification was most pronounced for grasslands (−9%), and significantly greater than that for croplands (−5%), plantations (−3%) and natural forests (−3%). The effect size for soil pH significantly decreased with increasing N-addition level and experimental duration.

3.3 | Soil C dynamics in response to soil acidification

When the changes in soil pH were divided into three levels, analyses revealed that the magnitude of soil acidification significantly affected the soil C pool and soil respiration (Figure 4). Concentration of SOC was significantly increased in mildly and severely acidified soil under N-addition treatments, but was slightly decreased in non-acidified soil (Figure 4a). The responses of MBC to N-induced soil acidification were exactly the opposite of those of SOC (Figure 4c). With the increasing magnitude of soil acidification, soil respiration and heterotrophic respiration showed decreasing trends (Figure 4d,e). However, autotrophic respiration significantly increased in both non-acidified and severely acidified soil under N-addition treatments (Figure 4f). Additionally, the effects of the magnitude of soil acidification on plant and microbial C-related variables are presented in Figure S8.

3.4 | Abiotic and biotic factors regulating soil C budget

Results indicated that the effect size of SOC significantly decreased with the litter mass (Figure 5a). The effect size of MBC and soil respiration appeared to increase with the litter mass (Figure 5b,c), but it was not statistically significant. The effect size of MBC

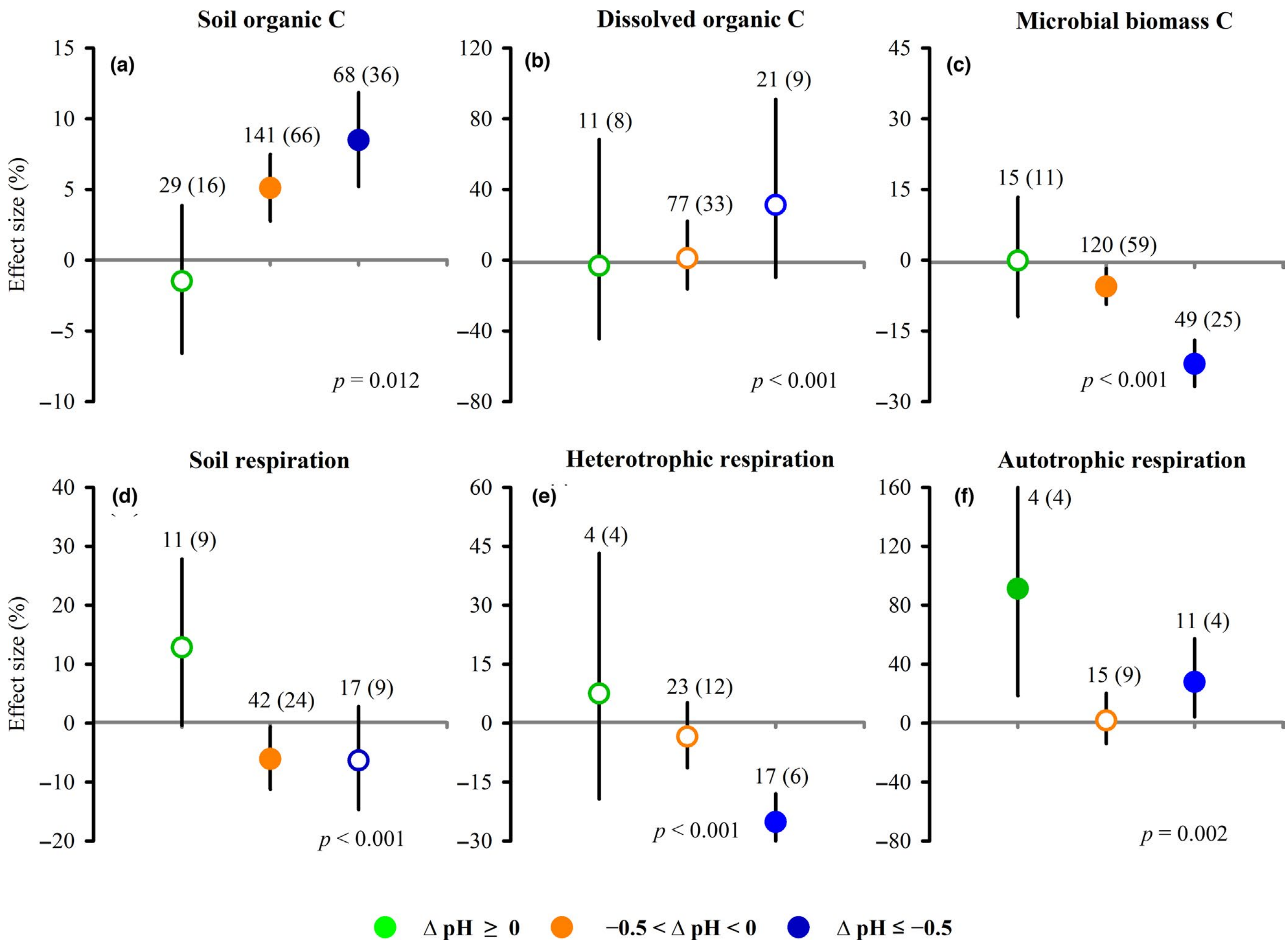

FIGURE 4 Concentrations of organic C and respiration in soil as affected by the magnitude of soil acidification caused by N-addition treatments. Note: Dots represent effect sizes with 95% confidence intervals (CIs). Values above the bars are the number of observations and studies (in brackets). Closed and open circles represent significant effects and insignificant effects, respectively

and soil respiration shifted positively with the fine root biomass (Figure 5e,f). For abiotic factors, the effect size of SOC increased linearly (Figure 5g), but the effect size of MBC and soil respiration decreased, with the reduced soil pH (Figure 5h,i). In addition, MAT and initial soil pH, but not MAP, significantly affected soil C dynamics (Figure S5).

4 | DISCUSSION

4.1 | Contrasting responses of plant–soil C dynamics

Nitrogen addition has been demonstrated to stimulate photosynthesis (Liang et al., 2020; Zhang, Li, et al., 2018). Being consistent with previous global meta-analyses (LeBauer & Treseder, 2008; Song et al., 2019), our results indicated that N enrichment strongly increased plant C fixation, via substantially increasing plant biomass in the terrestrial ecosystems of China (Figure 2a). Furthermore, fertilization regime significantly affected plant growth, with more pronounced responses in above-ground and root biomass as N additions and duration of experiments increased (Figure S3). Intriguingly, SOC concentration did not increase sharply (an average increase of 5%) in response to N-addition, despite increases in litter mass by 18% across the terrestrial ecosystems. Concentrations of SOC decreased linearly with increased litter mass, whereas MBC and soil respiration responded positively to increased below-ground C inputs (Figure 5a–f). Our results suggest that increased plant biomass resulting from N-addition may increase organic matter inputs to soil, but may also increase C loss from soil by increasing microbial C utilization, supporting, in part, the priming effect (Cheng et al., 2014; Kuzyakov et al., 2000). It is likely that increased N availability and organic C inputs released soil microbes from N limitation and promoted microbial degradation of initial SOC, resulting in a decreased SOC concentration under N enrichment in some cases. Decoupling of above-ground and below-ground C-related processes has been reported by many field N-addition experiments and meta-analyses (Kazanski et al., 2019; Liu & Greaver, 2010; Song et al., 2019),

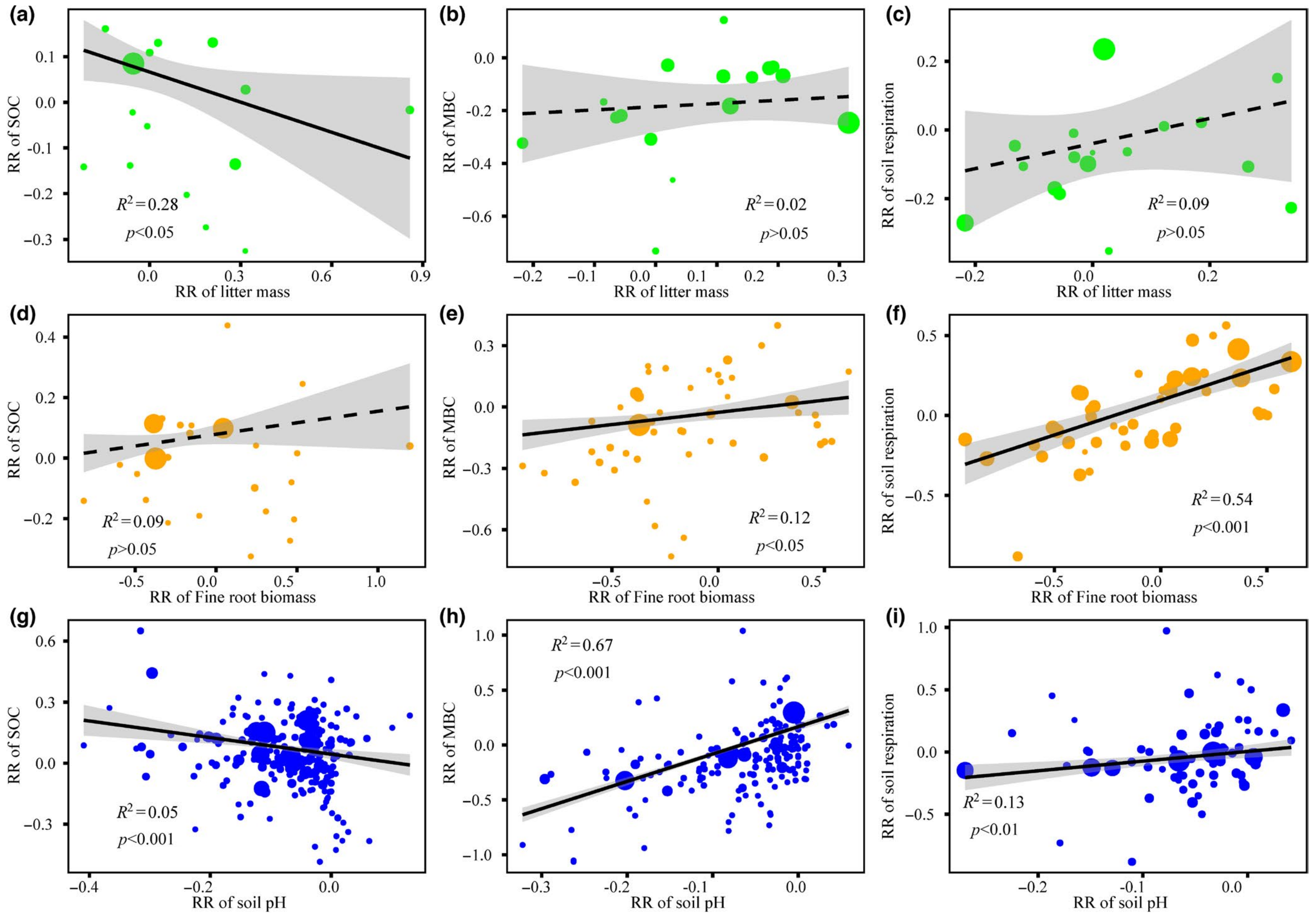

FIGURE 5 Relationships between the response ratio (RR) of soil C-related variables and abiotic/biotic factors. Linear regressions are shown as black solid lines and 95% confidence intervals are in the shaded area. The black dotted line represents a non-significant correlation. Each point represents the effect size of an individual study, and the size of bubbles represents the weight. See Figure 1 for abbreviations

indicating that soil C concentration does not always mirror above-ground C inputs.

Nitrogen addition also decreased C:N ratios in litter and fine roots, which is consistent with the findings of a recent global meta-analysis (Sun et al., 2020). Stoichiometric decomposition theory proposes that organic matter decomposition and utilization by soil micro-organisms are negatively related to the C:N ratio (Manzoni et al., 2012), and that labile C sources (i.e. sources with low C:N ratio) could enable micro-organisms to decompose native SOC to meet high N demands (Cheng et al., 2014). This hypothesis was supported by the negative correlation between SOC and organic matter inputs, and the positive correlation between MBC and organic matter in our study. It also suggests a plausible explanation for why the increasing above-ground biomass and labile C inputs did not sharply increase soil C concentration under N enrichment. We found, however, that MBC concentration, soil respiration and microbial biomass did not significantly increase in response to N-addition as expected (Figure 2), and other studies have found litter decomposition to decrease under N enrichment (van Diepen et al., 2015; Zhang, Luo, et al., 2018). Furthermore, the current meta-analysis (Figure 2b) and other meta-analyses (e.g. Lu, Guo, et al., 2021; Lu, Hou, et al., 2021; Xu et al., 2021) found that N-addition actually increases rather than reduces the SOC concentration despite increased inputs of labile C into soil. Clearly, the inputs of plant C may be not a primary determinant of below-ground C budget, suggesting an alternative explanation for increased SOC concentration under N enrichment.

4.2 | N-induced soil acidification hypothesis regulates soil C concentration

Soil acidification resulting from continuous N fertilization has been both a global environmental concern (Tian & Niu, 2015) and more specifically in China (Zhang et al., 2015). Our results revealed that experimental N-addition reduced soil pH by an average of 0.37 units (Figure 3), slightly greater than the decrease of 0.24 pH units reported in a global meta-analysis (Meng et al., 2019). The magnitude of soil acidification differed among ecosystem types, with N-mediated acidification more pronounced in grasslands and croplands than in other ecosystems in the current study

(Figure 3), consistent with those from previous studies of Chinese grasslands (−0.6 units) and croplands (−0.5 units) (Guo et al., 2010; Yang et al., 2012). These variations may be explained by differences in management practices, such as background fertilization, because grasslands and croplands have experienced severe human disturbance. In addition, the response of soil pH to N fertilization varied with fertilization rate, with rates of fertilization >50 kg N ha^{-1} $year^{-1}$ appearing as a threshold to initiate a response (Meng et al., 2019; Tian & Niu, 2015). Our results showed a marked decline in soil pH as the N-addition level increased. Tian and Niu (2015) found a non-significant effect of N-addition on soil pH when the experimental duration was longer than 20 years, suggesting that the effect of N-induced soil acidification on ecosystems diminished at long-term fertilization, due to the buffering by metal ions. In the current study, however, soil pH decreased with experimental durations. Further research is needed to determine the underlying mechanisms of soil acidification responding to long-term N-addition.

Although many studies have explained the impacts of N-addition on below-ground C accumulation by focusing on biotic factors, our results demonstrated that N-addition-induced soil acidification directly affected soil C-related processes (Figures 4 and 5). In non-acidified soils, N-addition increased the concentration of MBC and soil respiration and slightly decreased SOC concentrations, as expected. By contrast, in mildly and severely acidified soil, N-addition decreased the concentration of MBC and soil respiration, resulting in SOC accumulation. These results are supported by the hypothesis proposed by Averill and Waring (2018). That is, increasing soil acidification caused by N enrichment will decrease microbial production and limit microbial growth, thereby enhancing the accumulation of SOC. Furthermore, we found that heterotrophic respiration significantly decreased with decreasing soil pH in severely acidified soils, but autotrophic respiration significantly increased in both non-acidified and severely acidified soils (Figure 4e,f). Previous studies have found that the response of heterotrophic respiration to N enrichment was correlated with that of MBC, and that autotrophic respiration was mainly driven by fine root production (Liu & Greaver, 2010). Working with cropland soil, Chen et al. (2018) found that N-induced soil acidification reduced soil C loss by limiting microbial respiration rather than by limiting root respiration, and that apparently unaltered soil respiration could be caused by a balance of heterotrophic respiration inhibition by autotrophic respiration stimulation under N enrichment.

Convincing evidence indicates that the responses of extracellular enzyme activities to N-addition help explain why microbial C utilization is limited under soil acidification (Bonner et al., 2019; Waldrop et al., 2004). It is well known that microbial degradation involves multiple microbial enzymes. Hydrolytic enzymes (e.g. β-glucosidase) generally degrade simple compounds, whereas oxidative enzymes (e.g. peroxidase and polyphenol oxidase) are generally responsible for the decomposition of recalcitrant compounds (Carrara et al., 2018). Although N enrichment can promote the degradation of simple compounds, reduced soil pH can inhibit the microbial utilization of recalcitrant compounds (Bonner et al., 2019). Such changes in enzyme activities with N enrichment were documented in the

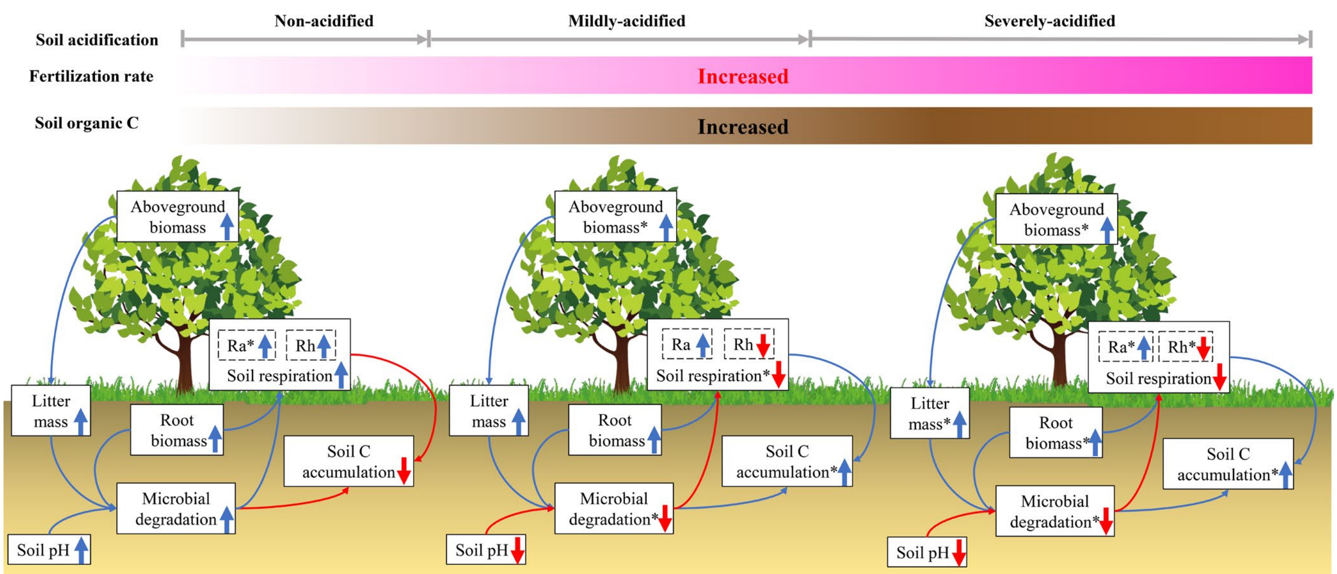

FIGURE 6 Conceptual model describing the responses of soil C-related processes in response to N-addition and the potential mechanisms involved in the regulation of soil C accumulation by acidification in terrestrial ecosystems. Blue and red arrows indicate variables that are positively and negatively altered by N-addition, respectively. Asterisks indicate statistically significant effects ($p < 0.05$), as per our meta-analysis. In response to non-acidified soil (towards the left side of the figure), N-addition promotes plant growth and increases the inputs of labile C into soils, stimulating soil C loss by soil microbial degradation, and hence reducing the accumulation of soil organic C. Over mild and severe soil acidification (towards the middle and right side of the figure), in contrast, the concentration of soil organic C increases because soil pH declines and limits microbial degradation of C

current (Figure 2c) and in previous meta-analysis (Jia et al., 2020; Jian et al., 2016). On the other hand, recent studies have reported that increased physical protection of soil aggregates caused by soil acidification promotes soil C accumulation (Lu, Guo, et al., 2021; Lu, Hou, et al., 2021; Ye et al., 2018). With increased soil acidification, N-addition can stimulate the formation of soil aggregates that help protect litter against microbial decomposition (Blanco-Canqui & Lal, 2004; Lu, Guo, et al., 2021; Lu, Hou, et al., 2021). Our meta-analysis revealed that concentrations of DOC tended to increase as soil pH decreased (Figure 4b), indicating that soil acidification increased the retention of labile organic C, again consistent with many previous studies (e.g. Hagedorn et al., 2015; Xu et al., 2021). The opposite responses of MBC and DOC to decreasing soil pH provided further support for pH regulation of SOC accumulation.

In addition, previous meta-analyses have shown that terrestrial C dynamics are significantly affected by environmental factors (e.g. MAT, MAP, soil type; Deng et al., 2018; Song et al., 2019). Our study comprised a wide range of physiographic conditions in China, with responses of C-related processes (e.g. organic matter inputs, SOC concentration and microbial characteristics) to N-addition varying among ecosystem types (Table S1). Temperature and precipitation have been reported to alter root traits (Li et al., 2015), litter decomposition (Zhang, Luo, et al., 2018) and microbial biomass under N enrichment (Jia et al., 2020). Regression analysis showed that the responses of SOC, MBC and soil respiration increased linearly with MAT, but were not closely associated with MAP (Figure S5), indicating that the responses of soil C dynamics to N-addition are sensitive to the temperature. With the increase in temperature, we suggest that the loss of soil C would enhance by increasing microbial activities, and hence decreased SOC. Consistent with other studies (Lucas et al., 2011; Zhang et al., 2020), we found that the responses of SOC and MBC increased linearly with initial soil pH (Figure S5g,h). The acid buffering capacity of soil depends on soil pH, soils with high initial pH values are more vulnerable to acidification than soils with low initial pH values (Meng et al., 2019). Therefore, the inter-site variation in initial pH values may affect the effect magnitude of N-addition on soil C accumulation. Briefly, these results demonstrate that ambient condition is a non-negligible factor for assessing soil C dynamics under N enrichment, and low temperature and low soil pH help to accumulate SOC.

4.3 | Implication for future research

Based on our synthesis of the effects of experimental N-addition on soil C-related processes in the terrestrial ecosystems in China, we developed a schematic model to explain the impacts of N on soil C budget and to illustrate the underlying mechanisms for how N-addition-induced soil acidification regulates SOC accumulation (Figure 6).

In conclusion, our meta-analysis highlights that substantial increases in plant C inputs do not determine SOC budgets under N enrichment due to the decoupling of above-ground–below-ground C dynamics. We suggest that N-induced soil acidification is a primary regulator of SOC in terrestrial ecosystems of China. N-addition is likely to stimulate microbial decomposition and increases soil C loss by increased C inputs at the initial stage, but this can be reversed by the decline in soil pH caused by a chronic input of high quantities of N. Thus, the magnitude of soil acidification regulates and drives SOC in the terrestrial ecosystems of China. These findings help reconcile many competing hypotheses on this widely debated topic. Additionally, it should be noted that the enhanced C concentration to terrestrial soils via N-manipulation experiments does not justify that anthropogenic N emissions could contribute to C neutrality, since the N-addition rate in most field experiments was much greater than the average rates of global N deposition (Song et al., 2019). On the contrary, our results suggest that, at present, chronic N deposition might increase atmospheric CO_2 by increasing losses of soil C via the stimulation of microbial degradation.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

X.L. and J.G. collected the data, performed the modelling work and analysed the output data; X.L. and E.H. performed the meta-analysis; Y.K., X.L. and F.S.G. wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via Figshare https://doi.org/10.6084/m9.figshare.16987921 (Lu, Guo, et al., 2021).

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