






Nitrogen deposition mitigates long-term phosphorus input-induced stimulative effects on soil respiration in a tropical forest

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ABSTRACT

Atmospheric nitrogen (N) deposition and anthropogenic phosphorus (P) input simultaneously affect soil respiration (R_S), a crucial process that mediates soil carbon (C) cycling. However, the interaction of N deposition and anthropogenic P input on R_S , as well as its components—autotrophic respiration (R_A) and heterotrophic respiration (R_H)—remain largely unexplored. Herein, we conducted an 8-year field experiment with N and P additions in a tropical secondary forest, integrating the vegetation traits, soil physicochemical properties, organic C fractions, and microbial properties, to explore the effects of nutrient inputs and their interactions on R_S , R_A , and R_H . Over eight years, along P input significantly increased R_S by 19.2% and R_H by 42.1%. These increases were partially mitigated (by 33.2% annually for R_S and 58.3% annually for R_H) with the addition of N. In contrast, the co-addition of N and P enhanced R_A compared to alone N or P addition, suggesting that N deposition mitigated the stimulative effect of P input on R_S by reducing R_H rather than R_A . The structural equation model further revealed that N deposition reduced R_H primarily by increasing soil N:P ratio and decreasing both the labile C fraction and fungi biomass. Our findings suggest that prevalent N deposition across low latitudes could have substantially mitigate C emissions from forest soils under anthropogenic P input.

1. Introduction

Tropical forest soils store about one-third of the world's soil carbon (C), totaling nearly 860 Pg C, which is three times the C present in Earth's atmosphere (Bonan, 2008; Pan et al., 2011). Soil respiration (R_S), encompassing autotrophic respiration (R_A) and heterotrophic respiration (R_H), is the principal pathway by which C fixed in the soil re-

leases into the atmosphere (Schindlbacher et al., 2009; Subke et al., 2006; Wang et al., 2022a). Thus, even minor fluctuations in R_S could influence atmospheric CO_2 levels and potentially accelerate climate change (Bond-Lamberty and Thomson, 2010). Both theoretical and empirical evidence indicate that soil nutrient availability significantly regulates R_S by influencing key biogeochemical processes, such as organic matter input, microbial metabolism, or energy production

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(Forsmark et al., 2020; Ma et al., 2022; Zhang and Shanguan, 2023a). However, the implications of interactions between multiple nutrients on R_S remain largely elusive. To precisely predict the tropical forest C cycle's response to anthropogenic nutrient inputs and global environmental change, it is crucial to understand these nutrient interactions on R_S and its components.

The significant increase in reactive phosphorus (P) inputs, stemming from the increased use of fossil fuels and intensive application of fertilizers, has substantially raised global P inputs into terrestrial ecosystems over the past century (Demay et al., 2023; Lu and Tian, 2017; Wang et al., 2021). Especially, the cumulative input of P has exceeded that of nitrogen (N) deposition in certain tropical regions, disrupting N:P ratio in both soils and organisms. This imbalance has, in turn, influenced nutrient-driven R_S (Das et al., 2013; Pett-Ridge, 2009; Ringeval et al., 2024). Studies have suggested that an increase in P input can enhance R_S in tropical forests by boosting microbial biomass and promoting soil organic carbon (SOC) decomposition (Fang et al., 2019; Hicks et al., 2019; Ma et al., 2022). This occurs because additional P alleviates microbial P limitation, fostering plant growth and microbial activity in P-limited tropical forests (Cui et al., 2022; Shi et al., 2024), which accelerates SOC decomposition and raises R_S (Li et al., 2024a; Xu et al., 2022). Moreover, P addition can elevate soil pH, alter soil structure, and improve soil aeration and water-holding capacity, further stimulating microbial activity and CO₂ release (Amarh et al., 2021; Fan et al., 2020; Shi et al., 2021). However, most studies have typically only conducted short-term (less than 5 years) P addition treatments, and the effects of long-term P input on R_S , especially its components (i.e., R_A and R_H), have been rarely examined in forest ecosystems.

In contrast to P input, long-term N deposition tends to decrease R_S by affecting vegetation traits, soil C quality, and microbial community composition under N-saturated conditions (Amarh et al., 2021; Li et al., 2022a; Zhang et al., 2021). For example, in tropical forests where N is often in excess, an increase in N can lead to nutrient imbalances, particularly by reducing the availability of essential nutrients such as P and potassium (Manu et al., 2024; Zhu et al., 2022). This imbalance can limit plant nutrient uptake, impairing plant growth and resulting in reduced litter production. The resulting lower quantity and quality of litter may further contribute to a decline in R_S (Peng et al., 2020; Wang et al., 2022b). Additionally, N addition in N-enriched ecosystems could result in soil acidification and a reduction in soil C quality (e.g., a decrease in labile organic C), which may inhibit SOC decomposition and further suppress R_S (Li et al., 2022b; Lu et al., 2014; Mao et al., 2017). Furthermore, N enrichment can intensify competition for P between plants and microorganisms, potentially reducing microbial biomass and thereby decreasing R_S (Fetzer et al., 2024; Siah et al., 2023; Zhang et al., 2023b). Nevertheless, whether long-term N deposition can counteract the stimulation of P input on R_S remains to be determined. Long-term N addition may produce more complex and potentially diverse effects, as it could alter soil microbial communities, soil pH, and nutrient balance due to ecosystem adjustments over time. Additionally, the mechanisms by which N deposition regulates R_S dynamics under long-term P input in forest ecosystems have not been extensively explored.

Tropical secondary forests are characterized by large C storage and significant CO₂ emissions (Aryal et al., 2017). These forests are also often exposed to high N deposition and long-term P input due to both natural and anthropogenic factors (Chen et al., 2023; Ma et al., 2022). To explore the potential effect of N deposition on CO₂ emissions from tropical forest soils under long-term P input, we conducted a long-term field experiment in a typical tropical secondary forest. We assessed changes in R_S and its components (R_A and R_H) in response to nutrient additions and their interactions, and examined how R_S responded to variations in vegetational (e.g., litter input), edaphic (e.g., C quality), and microbial (e.g., community composition) parameters. We hypothesized that: (1) P input would stimulate R_S by increasing both R_H and R_A in the soils, as P can promote plant growth in tropical forests (Ma et al., 2022); (2) N deposition would mitigate the stimulation of P input on R_S ,

as N deposition may suppress soil respiration in N-saturated conditions (Forsmark et al., 2020); (3) changes in R_S due to N deposition, in the context of long-term P input, would be correlated with the alterations in litter input, soil C quality, and fungi biomass.

2. Material and methods

2.1. Study area and experimental design

The study was conducted in a tropical forest (21°27'0" N, 110°54'0" E) at Xiaoliang Research Station in the Guangdong Province, China. This area is characterized by a tropical monsoon climate, with an average annual temperature of 23 °C and an average annual precipitation of 1400–1700 mm from 1975 to 2017. The area has a distinct seasonal pattern in which rainfall is mainly concentrated from April to October (70 %). The soil type in this area, as classified by the Soil Taxonomic System of China, is latosol (Lu et al., 2023). The forest was a typical evergreen broadleaf secondary forest (Mo et al., 2019).

In September 2009, six randomized blocks, each separated by a minimum distance of 50 m, were carefully selected for a fertilization study. These blocks shared similar vegetation type, geomorphology, lithology, soil type, and slope. In each block, a control group (CK) and three experimental treatments—N addition (+N), P addition (+P), and a combined N and P addition (+NP)—were allocated to three 10 m × 10 m plots. To prevent the inter-plot transfer of nutrients through fine roots, a 2-m buffer transect was established around each plot, along with edges that were trenched to a depth of 20 cm using polyvinyl chloride (PVC) plates. Beginning in September 2009, fertilizers were applied to the +N, +P, and +NP plots by dissolving 476.6 g of ammonium nitrate and/or 808 g of sodium dihydrogen phosphate in 30 L of groundwater. This solution was then applied every two months using a knapsack sprayer. The total N and/or P application rates were 100 kg ha⁻¹ year⁻¹ for each plot. For the control plots, 30 L of groundwater was simply added as a baseline treatment (Li et al., 2023).

2.2. Measurements of R_A and R_H

R_A and R_H were estimated using the trench method, which has been extensively employed in prior research (Zhou et al., 2020). Specifically, two subplots (1 m × 1 m) within each plot were randomly chosen. In one subplot, a root exclusion treatment was implemented in April 2009 using a 50 × 50 cm (length × width) PVC plate inserted to a depth of 60 cm. To monitor and maintain the integrity of the installation, regular inspections were conducted throughout the study period. Since plant roots in this study area were mainly concentrated in the topsoil layer up to 50 cm (Lu et al., 2023), the 60 cm PVC plate was intended to prevent viable root growth. At each subplot, a PVC collar (5 cm in height) was vertically sank into the soil at a 2 cm depth. To account for above-ground plant respiration, plants within the collars were carefully removed 24 h before measuring CO₂ fluxes. Soil respiration encompassed the combined respiratory activity of roots and microorganisms (Subke et al., 2006). Annual cumulative R_S and R_H (M) (g C m⁻² yr⁻¹) were estimated as:

$$M = \Sigma(R_{i+1} + R_i)/2 \times (t_{i+1} - t_i) \times 3600 \times 24 \times 10^{-2}$$

where R represents the rates of R_S or R_H (μmol m⁻² s⁻¹), and i and t refer to sampling number and sampling duration (days), respectively. R_A , which represents the respiration of live roots (Zhou et al., 2013), was derived by subtracting R_H from the total R_S . To ensure the effectiveness of nutrient addition treatments and the complete decomposition of dead roots, we began recording CO₂ fluxes in 2015, approximately six years after installation of the PVC collars.

Soil and microbial respiration were measured bi-monthly from July 2015 to July 2017 between 9:00 and 11:30 AM throughout the study using a portable LI-8100 automated CO₂ flux system (LI-COR Ltd.,

Lincoln, NE, USA), coupled to a model 8100–103 chamber. During each measurement, the chamber was placed over the soil collars to ensure a tight seal. Once gas concentration fluctuations within the chamber stabilized, CO₂ levels were recorded continuously in 10 intervals of 120 s each. The average rate from these intervals was used to determine the R_S and R_H. To prevent the interference of precipitation, measurements were skipped within 48 h after rainfall and during rainfall events.

2.3. Plant litter, soil, and microbe sampling and analysis

In June 2015, litter collection frames (1 × 1 m²) were randomly placed at each plot. At the beginning of each month, litter within these frames was collected, dried, and weighed. The dried litter mass was used as an estimate of litter input per square meter for each treatment, denoted as M_L. Additionally, three random 30 × 30 cm² subplots per plot were selected to gather all surface litter. The collected litter was dried and its organic carbon content was measured to assess litter quality (Q_L).

Soil sampling was carried out between July 2015 and July 2017 to measure physicochemical properties, organic carbon fractions, and microbial community composition. In each plot, three soil cores (5 cm diameter) were randomly collected from the 0–20 cm layer and pooled as one composite sample after removing surface litter. Fine roots and stones were manually removed from each sample, which was then divided into three parts. The first part was stored at 4°C for measuring soil water content (SWC) and available nutrients. The second part was air-dried for analyzing other soil physicochemical properties and organic carbon fractions. The third part was freeze-drying at –20°C to preserve the microbial community structure and functional markers for determining phospholipid fatty acids (PLFAs). Detailed analyses of soil properties, including SWC, SOC, soil total nitrogen (STN), soil total phosphorus (STP), dissolved organic carbon (DOC), ammonia nitrogen (NH₄⁺-N), and nitrate nitrogen (NO₃⁻-N), are provided in the [Supporting Information](#).

SOC quality was represented by labile organic carbon (LOC) and recalcitrant organic carbon (ROC). LOC, which includes DOC, microbial biomass carbon (MBC), and the light fraction of organic carbon (LFOC), is highly susceptible to microbial decomposition ([Shaver et al., 2006](#); [Song et al., 2024](#)). In contrast, ROC is resistant to decay ([Hartley and Ineson, 2008](#)). For methods of measuring MBC, please refer to the [Supporting Information](#). LFOC and heavy fraction organic carbon (HFOC) were isolated from soil samples using density fractionation ([Zhang et al., 2007](#)). Briefly, to separate LFOC from HFOC, soil samples were mixed with a NaI solution (density: 1.7 g cm⁻³) at a ratio of 50 ml per 15 g soil dry weight. This solution effectively differentiates the more labile LFOC from the more recalcitrant HFOC. The mixture was shaken for 30 min and centrifuged at 3000 rpm for 10 min, and then filtered through a 0.45 μm filter. The retained fraction was rinsed with 100 ml of 0.01 mol/L CaCl₂ solution and 150 ml of distilled water to remove NaI and CaCl₂. The residue was resuspended in NaI, stirred gently with a glass rod, and the process was repeated twice. Finally, the three sub-fractions were combined and oven-dried at 60°C. The LFOC was present in the suspended fraction, while the HFOC was found in the sediments collected from the centrifuge tubes.

ROC was determined using the chemical acid digestion method ([Rovira and Vallejo, 2002](#)). Specifically, 5 g of dry sediment that contained the HFOC fraction was transferred into a centrifuge tube and treated with 30 ml (6 mol/L) HCl. The mixture was incubated at 95°C for 16 h and then filtered. After removing residual HCl from the filter with deionized water, the filtrate was dried at 60°C. The soil organic carbon content of the dried sample was designated as ROC.

Soil microbial community composition was measured using PLFA analysis ([Frostegård et al., 2011](#)). Briefly, phospholipids were extracted from 8 g of frozen dry soil, then fractionated and quantified. The resultant fatty acid methyl esters (FAMES) were identified using a gas chromatograph (7890B, Agilent Technologies). The concentration of

each PLFA was correlated to the corresponding peak area. These peak areas were quantified in reference to the peak area of methyl nonadecanoate (19:0) which was previously added as internal standard ([Tunlid et al., 1989](#)). Microbial groups were categorized as total, fungi, arbuscular mycorrhizal fungi (AMF), saprotrophic fungi (SF), and bacteria based on their PLFA concentrations. A commercially available multi-standard (mix of FAMES) was used to identify the different PLFAs. The ratios of fungi PLFAs to bacteria PLFAs (F:B ratios) were calculated to further characterize the microbial community. Details of the PLFA biomarkers for each microbial group are provided in [Table S1](#).

2.4. Statistical analyses

Annual soil respiration fluxes were estimated by aggregating the cumulative soil respiration values derived from bi-monthly measurements over the entire year. Statistical analyses were performed using R version 4.1.3 and Amos 26.0 software. Repeated-measures analyses of variance (ANOVA) were performed to test the effects of nutrient addition, sampling time, and their interactions on R_S, R_A, and R_H. One-way ANOVA in conjunction with the Tukey's test was performed to explore the variations in the annual cumulative fluxes of R_S, R_A, and R_H, as well as vegetation traits, soil physicochemical properties, organic C fractions, and microbial community composition under CK and treatments of + N, + P, and + NP. Linear regression analyses were conducted to determine the correlations of R_H with organic C fractions and microbial properties. To determine the main predictors for R_H, random forest model was used to distinguish the relative importance of each explanatory variable. Variation partitioning analysis (VPA) was used to quantify the separate contribution of vegetation traits (M_L and Q_L), soil physicochemical properties (SWC, SOC, STN, STP, SOC:STN, SOC:STP, STN:STP, DOC, NH₄⁺-N, and NO₃⁻-N), organic C fractions (LOC and ROC), and microbial community composition (total, fungal, AMF, SF, bacterial, and F:B ratios PLFAs) in regulating R_H, using the *rdacca.hp* function in R "rdacca.hp" package. Differences were considered to be significant at a level of $p < 0.05$.

Structural equation model (SEM) was conducted to explore the regulatory mechanisms of N and P additions affecting R_A, R_H, and R_S. Prior to analysis, a theoretical model was developed to account for the hypothesized causal relationships among environmental variables ([Fig. S1](#)). Non-significant paths were systematically removed until the model achieved the best fit ([Zhang et al., 2022](#)). In the final model, we incorporated the N and P addition as influencing factors, with STN:STP, M_L, fungi, and LOC representing soil physicochemical properties, vegetation traits, microbial community composition, and soil C fractions, respectively.

3. Results

3.1. Effects of nutrient additions on soil respiration

Treatment, sampling time, and their interaction significantly affected R_S, R_A, and R_H ([Fig. 1](#)). Compared with the control, P addition significantly increased the annual cumulative R_S by 19.2 % and R_H by 42.1 %, while decreasing R_A by 49.8 %. N addition did not significantly alter the annual cumulative R_S, R_A, or R_H. N and P co-addition significantly reduced the annual cumulative R_S and R_H by 14.0 % and 16.2 %, respectively. Compared with the P addition, the N and P co-addition decreased the annual cumulative R_S by 33.2 % and R_H by 58.3 %, while increasing R_A. This suggests that N addition primarily mitigates R_S by reducing R_H. All respiration rates exhibited seasonal variation, with lower values observed during the non-growing season (November–April) and maximum rates occurring during the growing season (May–October) ([Fig. 1a, b, & c](#) and [Table S2](#)).

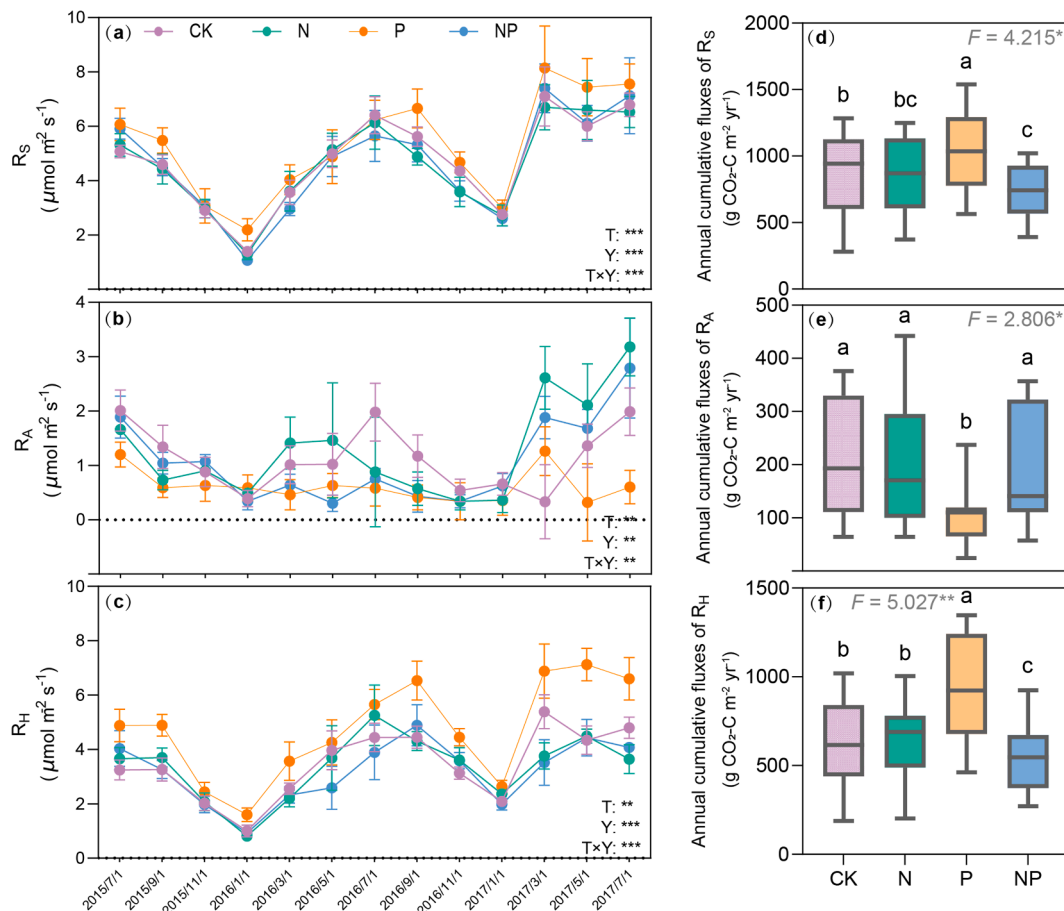


Fig. 1. Effects of N addition, P addition, and the combination of N and P co-additions on temporal variations in (a) soil respiration rate (R_s), (b) autotrophic respiration rate (R_A), (c) heterotrophic respiration rate (R_H) and annual cumulative in (d) R_s , (e) R_A , and (f) R_H in a tropical secondary forest. CK: control; N: N addition; P: P addition; NP: N and P co-addition. Each box denotes the interquartile range, the whiskers denote the minimum value, and horizontal line denotes the median. Different lowercase letters indicate significant differences between N and/or P additions and control. *, **, ***, and ns represent significant differences at $P < 0.05$, $P < 0.01$, $P < 0.001$, and $P > 0.05$, respectively.

3.2. Vegetation traits and soil physicochemical properties

Nutrient additions significantly affected STP, SOC:STP, STN:STP, and DOC, but did not impact M_L , Q_L , SWC, SOC, STN, SOC:STN, NH_4^+-N , and NO_3^-N ($P > 0.05$) (Table 1). Specifically, with P addition, STP and DOC increased by 84.4 % and 23.3 %, respectively, while SOC:STP and STN:STP decreased by 53.9 % and 57.6 %, respectively ($P < 0.05$). N addition significantly increased DOC by 21.92 %. N and P co-addition enhanced STP, whereas decreased SOC:STP and STN:STP (Table 1).

3.3. Soil organic C fractions and microbial community composition

Soil LOC was significantly higher under P addition (Fig. 2a), while there was no significant difference in the ROC among different nutrient treatments (Fig. 2b). Soil AMF and SF varied significantly with nutrient additions (Fig. 3c, & d). In detail, AMF under P addition was significantly higher than other three treatments (Fig. 3c). N and P co-addition significantly increased SF, but the individual effects of N and P were weak (Fig. 3d). However, there were no significant differences in the total, fungal, and bacterial PLFAs and F:B ratios among different nutrient additions (Fig. 3a, b, e, & f).

3.4. Potential mechanisms driving soil respiration

Linear regression analysis indicated a positive correlation between R_H and M_L , LOC and total, fungi, AMF, and SF PLFAs (Fig. 4). The key

factors for predicting R_H included STN:STP, M_L , DOC, LOC, NO_3^-N , SF, fungi, and AMF (Fig. 5a and Table S3). VPA showed that soil physicochemical properties, vegetation traits, soil C fractions, and microbial properties collectively explained 59 % of variation in R_H (Fig. 5b). Further, microbial properties played a dominant role in regulating R_H , followed by soil physicochemical properties and soil C fractions. SEM analysis revealed that N addition regulated R_H under P input by directly influencing STN:STP and M_L , and indirectly altering fungi and LOC (Fig. 6). Overall, N addition mitigated the stimulative effect of P input on soil R_s , primarily by regulating R_H , through an increased N:P ratio and an decrease in fungi biomass and LOC.

4. Discussion

4.1. Long-term P input increases soil R_H but reduces R_A

Our findings reveal that long-term P addition markedly elevated R_s only by increasing R_H (Fig. 1), partially supporting our first hypothesis. The increase in R_H could be attributed to two ways. First, P is a crucial nutrient that limits plant growth and root biomass in tropical forests (Mo et al., 2019; Wright, 2019). The application of P enhances plant productivity and the input of plant-derived C (Table 1), providing a plentiful substrate for decomposition and consequently increasing R_H (Baah-Acheamfour et al., 2020). Second, P addition impacts the microbial biomass in the soil (Fig. 3), specifically favoring organisms that are efficient at extracting and utilizing P (Ma et al., 2021; Ma et al., 2020).

Table 1

Effects of N addition, P addition, and the combination of N and P co-additions on vegetation traits and soil physicochemical properties in a tropical secondary forest.

Variables	CK	N	P	NP	F	P
M_L (g/m ² (- -))	89.51 ± 9.16a	71.06 ± 4.01a	59.99 ± 2.56a	73.46 ± 3.77a	0.847	0.484
Q_L (%)	38.07 ± 3.64a	38.34 ± 2.63a	39.71 ± 2.15a	40.70 ± 1.76a	1.080	0.380
SWC (%)	20.82 ± 2.92a	22.94 ± 0.72a	21.97 ± 0.93a	21.82 ± 1.04a	1.374	0.280
SOC (g kg ⁻¹)	28.83 ± 6.41a	24.84 ± 5.38a	26.25 ± 6.08a	25.73 ± 4.64a	0.458	0.715
STN (g kg ⁻¹)	1.39 ± 0.14a	1.48 ± 0.53a	1.15 ± 0.20a	1.61 ± 0.48a	1.263	0.314
STP (g kg ⁻¹)	0.22 ± 0.05b	0.22 ± 0.04b	0.40 ± 0.04a	0.45 ± 0.08a	24.670	0.000
SOC:STN	21.59 ± 3.55a	17.72 ± 3.60a	23.43 ± 6.70a	17.96 ± 7.03a	1.195	0.337
SOC:STP	145.31 ± 53.00a	112.49 ± 15.91a	67.03 ± 18.09b	58.61 ± 14.31b	9.164	0.000
STN:STP	6.92 ± 2.05a	6.56 ± 1.37a	2.94 ± 0.58b	3.53 ± 0.75b	11.95	0.000
DOC (g kg ⁻¹)	0.73 ± 0.10b	0.89 ± 0.12a	0.90 ± 0.08a	0.85 ± 0.10ab	3.301	0.041
NH ₄ ⁺ -N (mg kg ⁻¹)	20.03 ± 6.04a	22.91 ± 3.81a	19.66 ± 2.06a	24.25 ± 9.64a	1.661	0.207
NO ₃ ⁻ -N (mg kg ⁻¹)	13.07 ± 2.13a	12.67 ± 0.70a	11.43 ± 2.24a	12.55 ± 1.88a	0.723	0.550

CK: control; N: N addition; P: P addition; NP: N and P co-addition. M_L : litter mass; Q_L : litter quality; SWC: soil water content; SOC: soil organic carbon; STN: soil total nitrogen; STP: soil total phosphorus; SOC:STN: the ratio of SOC to STN; SOC:STP: the ratio of SOC to STP; STN:STP: the ratio of STN to STP; DOC: Dissolved organic carbon; NH₄⁺-N: ammonia nitrogen; NO₃⁻-N: nitrate nitrogen. Values are the mean values ± standard deviations (n = 6). Different letters indicate significant differences between different treatments.

This increase in microbial biomass promotes the decomposition of SOC, further enhancing R_H . Our analysis indicated that soil fungi and AMF were positively correlated with R_H (Fig. 4f & g). Notably, their relative abundance increased significantly in response to P addition (Fig. 3b & c), suggesting a pivotal role in the C cycling process.

It was anticipated that P addition would lead to an increase R_A due to its positive influence on plant growth and fine root biomass. This anticipation was based on the common requirement for increased energy investment in root growth and maintenance in the face of higher nutrient availability (Liu et al., 2019). However, in conflict with the first hypothesis, our research revealed that P addition significantly reduced

R_A (Fig. 1 and Table S2). A likely explanation is that alleviating P limitation reduces the need for C allocation to roots for nutrient acquisition (Ven et al., 2019). When P becomes non-limiting, plants may adjust their C allocation strategies, directing less C towards nutrient acquisition and root respiration as the nutrient uptake efficiency improves (Meng et al., 2022). This reallocation of C resources could lead to a decreased investment in root metabolic activity, ultimately resulting in a reduction in R_A .

4.2. N deposition mitigates P input-induced stimulation of R_S

Our research corroborated our second hypothesis by demonstrating that N addition markedly mitigated the increase in R_S stimulated by anthropogenic P input in the tropical secondary forest (Fig. 1 and Table S2). This provides the first field-based evidence that forest management can mitigate the enhanced soil R_S resulting from P inputs, highlighting the importance of exploring how human activities modulate soil CO₂ emission under multiple global changes (Li et al., 2024b). Furthermore, given that previous studies have demonstrated that N application significantly boosts SOC stocks (Li et al., 2023a; Martinson et al., 2021; Xia et al., 2020), it suggests that N application could be an efficacious strategy for reducing soil C loss in tropical forests experiencing high P inputs. This approach could contribute to enhancing the C sequestration potential of these critical ecosystems and mitigating the effects of anthropogenic activities on the global C cycle.

4.3. Mechanisms of N deposition mitigating R_S

Our findings showed that N and P co-addition reduced R_H but increased R_A (Fig. 1 and Table S2). This pattern suggests that under long-term P input, N deposition primarily regulates CO₂ emissions from the soil by modulating R_H . Consistent with earlier investigations (Cisneros-Dozal et al., 2007; Zhuang et al., 2023), our study confirmed a strong correlation between R_H and M_L in the context of N and P co-addition (Figs. 4a & S2), supporting our third hypothesis. In P-limited tropical forests, N addition can alleviate the demand of plants for other essential nutrients, such as potassium (Naples and Fisk, 2010; Xiao et al., 2021). This reduced demand decreases nutrient uptake from the soil, which in turn slows litter decomposition and root exudate secretion. Furthermore, excessive N input may lead to soil acidification and reduced oxygen availability, further affecting the production of plant litter and root exudates (Li et al., 2022a; Lu et al., 2014; Mao et al., 2017). These changes reduce the available C sources for soil microbes, inhibiting their growth and metabolic activities, and ultimately leading to a decrease in R_H (Zhuang et al., 2023).

In line with our third hypothesis, we observed a positive correlation

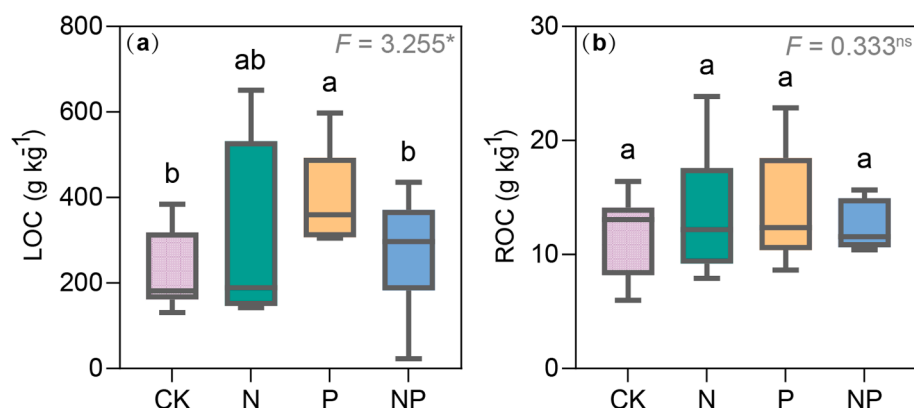


Fig. 2. Effects of N addition, P addition, and the combination of N and P co-additions on (a) labile organic carbon (LOC) and (b) recalcitrant organic carbon (ROC). CK: control; N: N addition; P: P addition; NP: N and P co-addition. Each box denotes the interquartile range, the whiskers denote the minimum value, and horizontal line denotes the median. Different lowercase letters indicate significant differences between N and/or P additions and control. *, **, ***, and ns represent significant differences at $P < 0.05$, $P < 0.01$, $P < 0.001$, and $P > 0.05$, respectively.

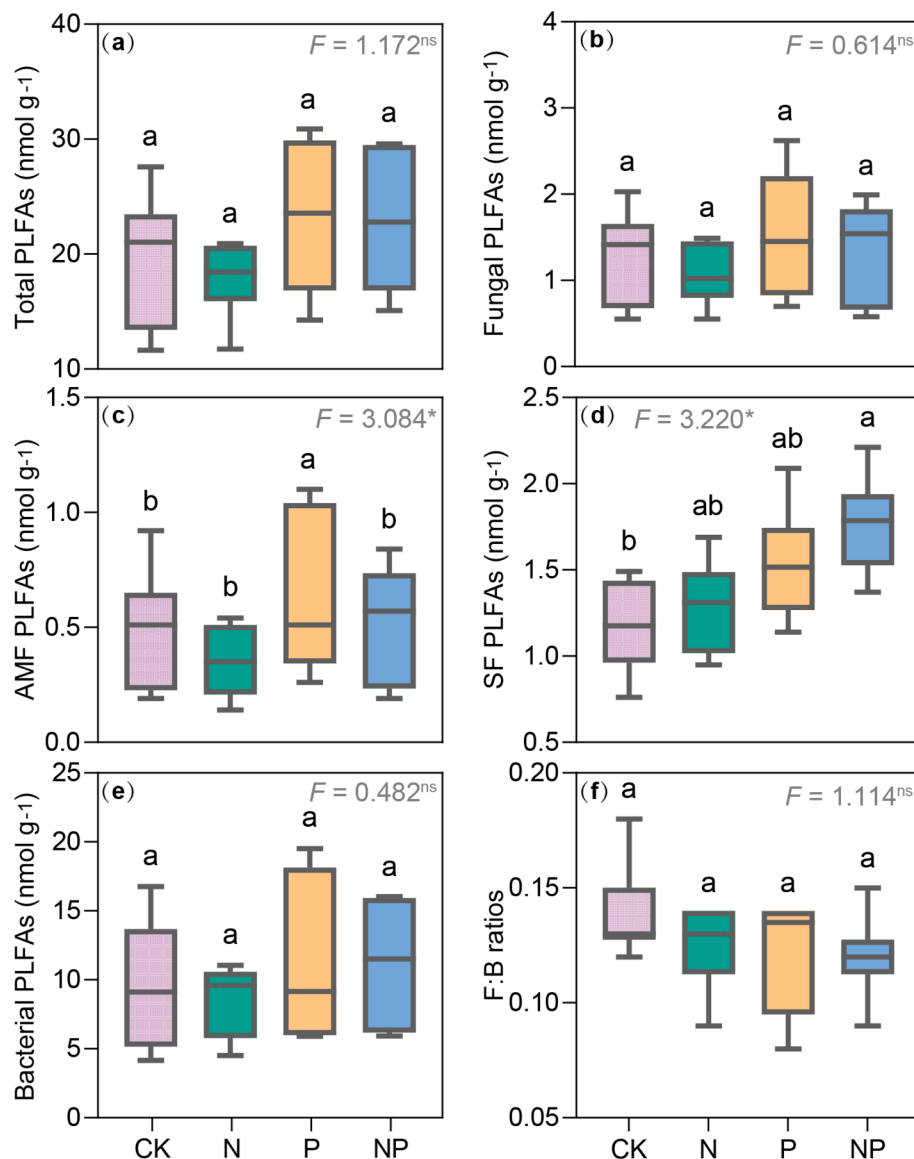


Fig. 3. Effects of N addition, P addition, and the combination of N and P co-additions on microbial community composition. (a) Total PLFAs, (b) fungal PLFAs, (c) arbuscular mycorrhizal fungi (AMF) PLFAs, (d) saprotrophic fungi (SF) PLFAs, (e) bacterial PLFAs, and (f) fungi:bacterial ratios (F:B ratios). CK: control; N: N addition; P: P addition; NP: N and P co-addition. Each box denotes the interquartile range, the whiskers denote the minimum value, and horizontal line denotes the median. Different lowercase letters indicate significant differences between N and/or P additions and control. * represent significant differences at $P < 0.05$.

between LOC and R_H in the presence of N and P additions (Fig. 4c & 6). LOC, unlike low-quality SOC, is more rapidly absorbed and utilized by microorganisms, thereby exerting a more potent influence on microbial respiration (Li et al., 2023b). In the current study, N addition inhibited plant growth and reduced litter production (Table 1), which decreased the input of actively decomposing organic matter into the soil. This resulted in a reduction in LOC content and a subsequent decline in R_H . These results highlight the importance of SOC quality in moderating C emissions from the soil (Ali et al., 2018; Li et al., 2022b).

Microbial community composition was also a crucial factor in regulating C emissions from the soil under varying nutrient conditions (Giles et al., 2023). Our study found a positive correlation between fungi and AMF with R_H under N addition (Fig. 4f, g, & 6), which aligns with our third hypothesis. This correlation can be attributed to the critical role fungi play in the decomposition of complex SOM (Moore et al., 2015). N deposition can decrease the proportion of fungi in the soil microbiome, thereby diminishing the microbial community's capacity to decompose persistent organic C (Li et al., 2024b; Zhou et al., 2020). Consequently, this leads to a decrease in R_H . These findings underscore

the importance of fungi communities in mediating soil respiration and C emissions from the soil under N deposition.

4.4. Implications and limitations

This study provides significant insights into the dynamic nature of C cycling in tropical secondary forests by examining the interactive effects of N deposition and P input on R_S and its components, R_A and R_H . These insights are crucial for informing environmental policies and management practices aimed at reducing soil C loss and balancing nutrient cycling in forest ecosystems. However, the study is limited by its focus on a specific tropical forest, which may not be representative of other ecosystems or climatic conditions. Additionally, although the 8-year experimental period provides valuable data, it may not fully capture longer-term ecological processes. The use of structural equation models, while effective, simplifies the complex interactions in tropical ecosystems, and factors such as climate variability were not thoroughly explored. Future research should aim to investigate these nutrient input effects across diverse ecosystems and over longer time scales to enhance

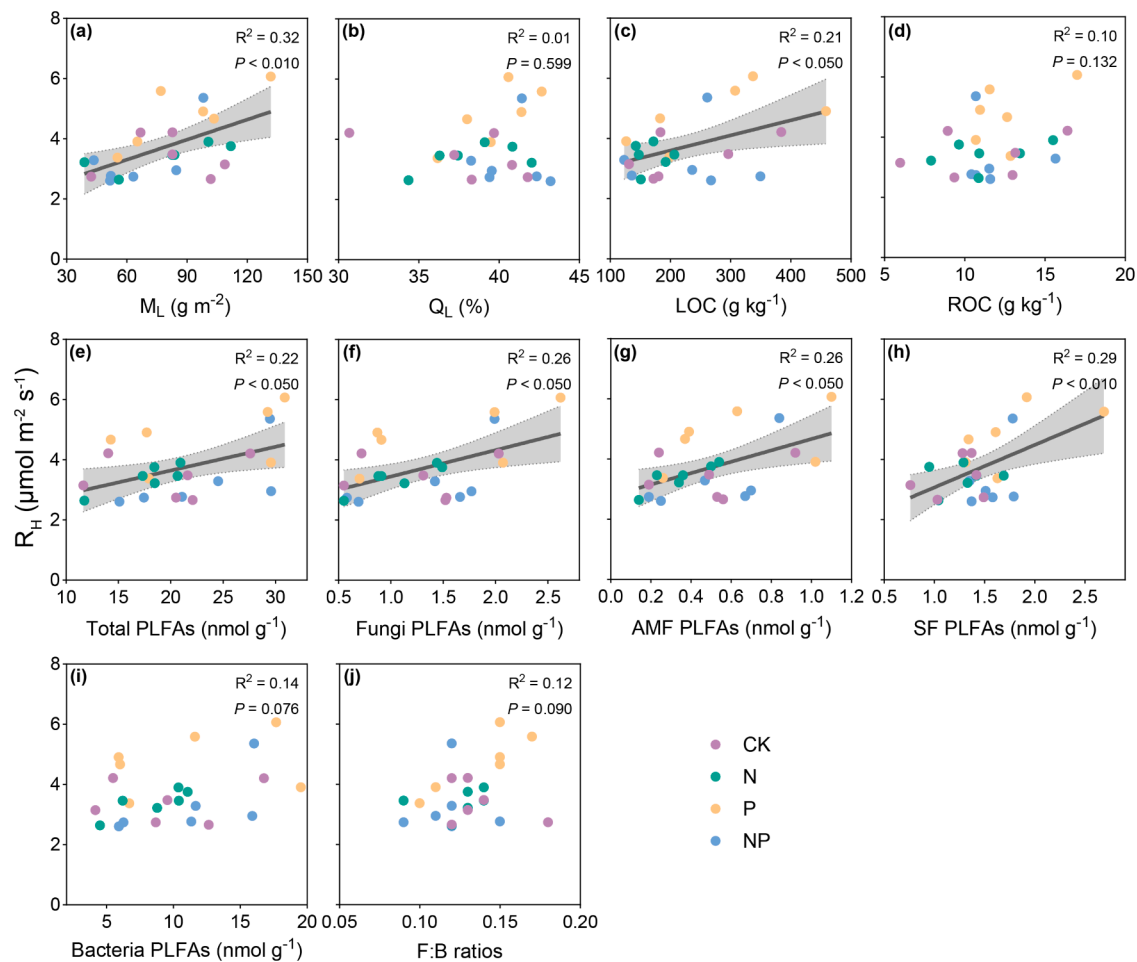


Fig. 4. Relationships between heterotrophic respiration rate (R_H) and soil carbon fractions and microbial community composition. M_L : litter mass; Q_L : litter quality; LOC: labile organic carbon; ROC: recalcitrant organic carbon; AMF: arbuscular mycorrhizal fungi; SF: saprotrophic fungi; F:B ratios: the ratios of fungi to bacteria.

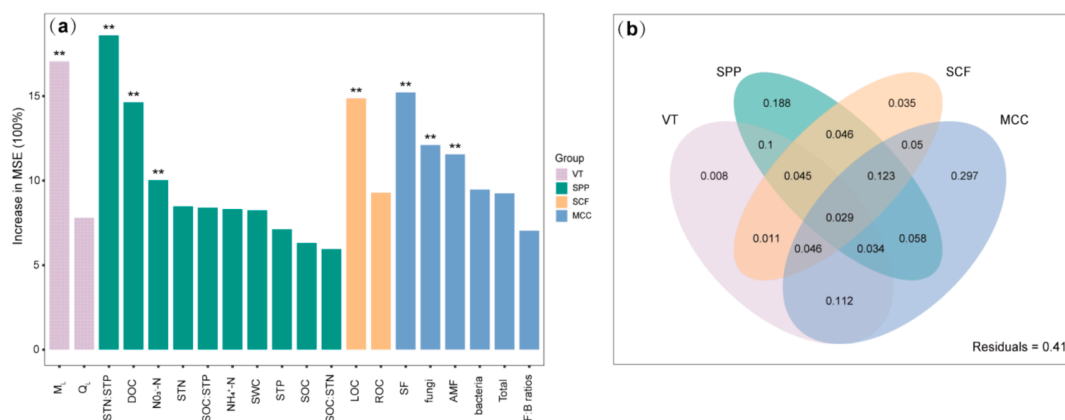


Fig. 5. Potential drivers for heterotrophic respiration rate (R_H). (a) Random forest analysis predicts the importance of variables in affecting R_H . Percentage increases in the MSE (mean squared error) of variables were used to estimate the importance of these predictors, and higher MSE% values imply more important predictors. Significance levels are as follows: *, $P < 0.050$; **, $P < 0.010$; and ***, $P < 0.001$. M_L : litter mass; Q_L : litter quality; SWC: soil water content; SOC: soil organic carbon; STN: soil total nitrogen; STP: soil total phosphorus; SOC:STN: the ratio of SOC to STN; SOC:STP: the ratio of SOC to STP; STN:STP: the ratio of STN to STP; DOC: Dissolved organic carbon; NH_4^+-N : ammonia nitrogen; $NO_3^- -N$: nitrate nitrogen; LOC: labile organic carbon; ROC: recalcitrant organic carbon; AMF: arbuscular mycorrhizal fungi; SF: saprotrophic fungi; F:B ratios: the ratios of fungi to bacteria. (b) Variation partitioning analysis (VPA) showing the respective effects of vegetation trait (VT: M_L and Q_L), soil physicochemical properties (SPP: SWC, SOC, STN, STP, SOC:STN, SOC:STP, STN:STP, DOC, NH_4^+-N , and $NO_3^- -N$), soil carbon fractions (SCF: LOC and ROC), and microbial community composition (MCC: Total PLFAs, fungi, AMF, SF, bacteria, and F:B ratios) on R_H .

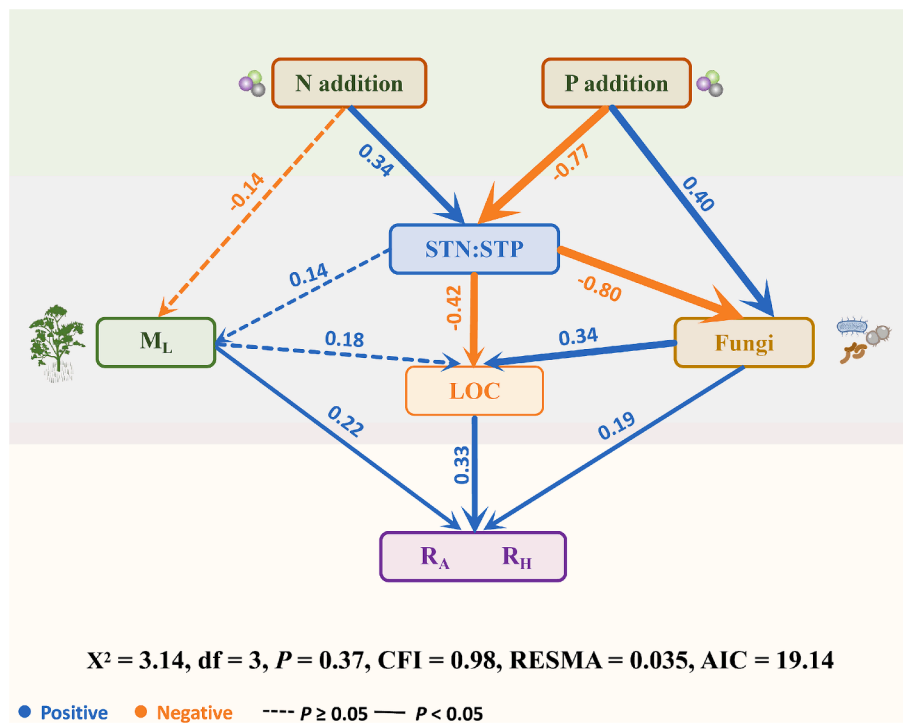


Fig. 6. Structural equation model (SEM) depicted the major pathways of N and P additions affecting autotrophic respiration rate (R_A), heterotrophic respiration rate (R_H), and soil respiration rate (R_S) ($n = 72$). A priori path modeling is shown in Fig. S1 (Supporting Information). The continuous and dashed arrows indicate significant and insignificant relationships, respectively. Blue and yellow arrows indicate positive and negative correlations, respectively. Numbers adjacent to arrows are standard path coefficients. STN:STP: the ratio of soil total nitrogen to soil total phosphorus; M_L : litter mass; LOC: labile organic carbon; Fungi: fungi biomass.

the generalizability of the findings.

5. Conclusions

Our research revealed that long-term P input significantly increased the annual R_S and R_H by 19.2 % and 42.1 %, respectively, over a 3-year experimental period in a tropic secondary forest. We also found that prevalent N deposition can substantially mitigate the stimulative effects of anthropogenic P input on R_S , primarily by reducing R_H through mechanisms such as increasing the soil N:P ratio and decreasing labile C fractions and fungal biomass. Our results provide insights into forest C cycling that the N deposition could mitigate the stimulation of P input to CO_2 emission from the soil. Overall, this study offers critical understanding of the interactive effects of N and P inputs on ecosystem processes, which help to balance nutrient cycling and reduce soil C loss. Future research should prioritize investigations within ecosystems characterized by varied climates and nutrient limitations, aiming to further examine the effects of human-induced nutrient inputs on soil respiration and C dynamics in terrestrial ecosystems.

CRedit authorship contribution statement

Kingyun Huang: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yingwen Li:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Shiqin Yu:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Yongxing Cui:** Writing – review & editing, Validation, Supervision, Software, Project administration, Investigation, Conceptualization. **Fangyuan Guan:** Writing – review & editing, Visualization, Software, Methodology,

Investigation, Formal analysis, Conceptualization. **Yongxing Li:** Writing – review & editing, Validation, Supervision, Software, Project administration, Investigation, Conceptualization. **Jingtao Wu:** Writing – review & editing, Visualization, Methodology, Investigation. **Yang Hu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software. **Zhian Li:** Writing – review & editing, Project administration, Methodology, Investigation. **Ping Zhuang:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation. **Bi Zou:** Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation. **Guoming Qin:** Writing – review & editing, Writing – original draft, Visualization, Software. **Jingfan Zhang:** Writing – review & editing, Writing – original draft, Visualization, Software. **Jinge Zhou:** Writing – review & editing, Writing – original draft, Visualization, Software. **Ruyi Ding:** Writing – review & editing, Writing – original draft, Visualization, Software. **Faming Wang:** Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2024.117142>.

Data availability

Data will be made available on request.

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