



Nitrogen and phosphorus addition exerted different influences on litter and soil carbon release in a tropical forest



Jingfan Zhang^{a,b,c}, Jinge Zhou^{a,b,c}, Hans Lambers^d, Yingwen Li^a, Yongxing Li^a, Guoming Qin^{a,b}, Mei Wang^e, Jun Wang^a, Zhian Li^{a,c}, Faming Wang^{a,c,*}

^a Xiaoliang Research Station of Tropical Coastal Ecosystems, Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, CAS engineering Laboratory for Ecological Restoration of Island and Coastal Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510000, PR China

^b University of Chinese Academy of Sciences, Beijing 100049, China

^c Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou 510000, PR China

^d School of Biological Sciences, The University of Western Australia, Crawley, Perth, WA 6009, Australia

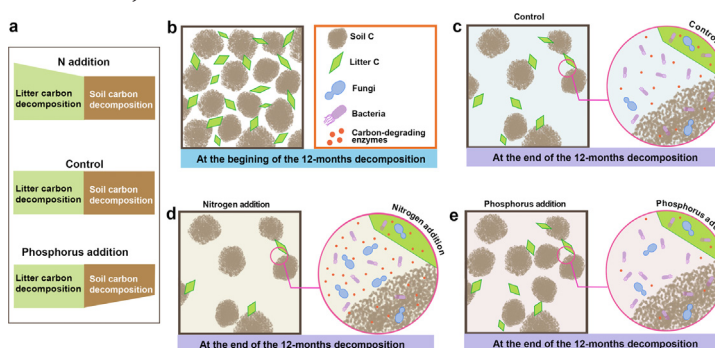
^e School of Geography, South China Normal University, Guangzhou 510631, PR China

HIGHLIGHTS

- Nitrogen (N) and phosphorus (P) selectively modify litter and soil C decomposition.
- N addition increased the litter carbon decomposition while P had no influence on it.
- P addition impeded the soil carbon decomposition while N had no influence on it.
- Litter P concentration played a vital role in litter decomposition.
- Greater C-release rate was attributed to higher microbial activities.

GRAPHICAL ABSTRACT

Conceptual diagrams showing how N and P addition modify the litter and soil C decomposition and the underlying microbial mechanisms. Panel (a) shows changes in the litter and soil decomposition under N and P addition. Panel (b) shows the relative amount of the soil carbon (C) and litter C at the beginning of the 12-months decomposition experiment in a tropical forest in south China. Panel (c) shows the relative amount of the soil C and litter C in unfertilized controls at the end of the decomposition experiment, where the enzyme activities and microbial community compositions in soils were shown in the circle; panel (d) shows nitrogen (N) addition enhanced the litter decomposition through the increased enzyme activities, fungal biomass, total PLFAs biomass (although the relative bacterial abundance were decreased); panel (e) shows phosphorus (P) addition impeded the soil C decomposition through the decreased C-degrading activities and total PLFAs biomass (although the relative bacterial abundance were increased).



ARTICLE INFO

Editor: Fang Wang

Keywords:

C release

South China

ABSTRACT

Terrestrial soils release large amount of carbon dioxide (CO₂) each year, which are mainly derived from litter and soil carbon (C) decomposition. Nutrient availability, especially nitrogen (N) and phosphorus (P), plays an important role in both litter and soil C decomposition. Therefore, understanding the underlying mechanism is crucial for mitigating CO₂ emission and climate changes. Here, we assessed patterns of litter and soil C decomposition after 11 yrs. in-situ N and P addition in a tropical forest where corn leaves or corn roots were added as litter C. The total CO₂ efflux was quantified

Abbreviations: SOC, soil organic carbon; SOM, soil organic matter; LOC, labile organic carbon; PLFAs, phospholipid fatty acids; POC, particulate organic carbon; MAOC, mineral-associated organic carbon.

* Corresponding author.

E-mail address: wangfm@scbg.ac.cn (F. Wang).

<http://dx.doi.org/10.1016/j.scitotenv.2022.155049>

Received 26 November 2021; Received in revised form 1 April 2022; Accepted 1 April 2022

Available online 4 April 2022

Mineralization
Decomposition
Soil microbial composition
Enzyme

and partitioned using ^{13}C isotope signatures to determine the sources (litter or soil C) every three months. In addition, Changes in C-degrading enzyme activities: β -1,4-glucosidase (BG), phenol oxidase (PHO) and peroxidase (PER), and microbial biomarkers were assessed to interpret the underlying mechanism. Total C-release was enhanced up to 17% by the long-term N addition but inhibited up to 15% by P addition. Precisely, N addition only accelerated the litter decomposition and increased about 42% and 6% of the litter C release at 0–5 cm and 5–10 cm soil depths, respectively; while P addition only impeded the soil C decomposition and decreased about 9% and 11% of the soil C release at 0–5 cm and 5–10 cm, respectively. The enhanced C release under N addition might be attributed to the enhanced microbial biomass, the ratio of fungi to bacteria and C-degrading enzyme activities. However, P addition resulted in the reverse result in microbial properties and C-degrading enzyme activities, associated with a decreased C release. Our study suggests that the long-term N and P addition selectively affected the litter and soil C decomposition because of their different physiochemical properties and this tendency might be more pronounced in tropical forests exposed to increasing atmospheric N deposition in the future. The study indicates that the different patterns of litter and soil C decomposition under climate change should be taken account in the future C management strategies.

1. Introduction

The soil is a major reservoir of potentially mineralizable carbon (C) and serves as a buffer against atmospheric carbon dioxide (CO_2) increase and a potential sink for additional C depending on the balance between photosynthesis, decomposer organism respiration and stabilizing C in soils (Chen, 2021; Dungait et al., 2012; Wang et al., 2021). Tropical forests represent a major terrestrial C stock, a large proportion of which is contained in the soil and decaying organic matter (Phillips et al., 1998; Grace et al., 2001; Guo and Gifford, 2010) and the turnover of organic C is fast in tropical forests (Ramankutty et al., 2002). There was considerable amount of CO_2 released from tropical forest soil floors and was mainly derived from litter and soil C decomposition (Sayer et al., 2011). Litter, forming the link between soil and vegetation, is key component of forest ecosystems (Zhou et al., 2017). Litter decomposition is a vital process in the global C balance and affected by both biotic and abiotic factors including litter quality, soil decomposer activity and nutrient availability (Berg et al., 2010; Garcia-Palacios et al., 2016). Multiple interactions between the Soil C and litter determines the turnover and storage of soil organic C (SOC), which are influenced by global changes (Crow et al., 2010). However, litter added to soils can also stimulate the soil C mineralization, a phenomenon known as the “priming effect” (Kuzyakov et al., 2000). Therefore, understanding the dynamics of litter and soil C decomposition is crucial for predicting the future terrestrial C release under climate change.

Nutrient availabilities, especially availability of nitrogen (N) and phosphorus (P), regulate litter and soil C decomposition as they can mediate microbial activities (Mackenzie et al., 2002; Jing et al., 2017). Globally, N and P are the most prevalent limiting nutrients for plant growth (Elser et al., 2007; Vitousek et al., 2010; Hou et al., 2020). Nutrient addition in terrestrial ecosystems may alter organic C decomposition through changes in degrading enzyme activities (Cusack, 2013), microbial community composition (Li et al., 2014) and microbial investment in enzyme production (Wang et al., 2020). Although there are numerous studies on how litter or soil C decomposition responds to elevated N levels, there is no clear consensus. A meta-analysis showed that N addition enhanced soil C turnover in short-term studies, while it slowed it down in long-term studies (Janssens et al., 2010). Moreover, in heavily N-limited ecosystems, soil C decomposition may be accelerated by greater N availability (Bragazza et al., 2012) via the increased microbial biomass and activity and the production of C-degrading enzymes (Manning et al., 2008). Different from soil C, which persists in soils through chemical bonding and physical protection (Koegele-Knabner et al., 2008), litters comprise freshly added organic matter, and have greater C and N concentrations, making them more accessible to microbial decomposition (Aerts, 1997). In addition to the microbial and enzymatic characteristics, the litter quality also plays a key role in affecting its decomposition. For example, high-quality (low-lignin) litter decomposition is stimulated by N addition ($<5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) across different ecosystems including forests and grasslands, while similar patterns were not observed with low-quality litter (Knorr et al., 2005). Furthermore, the response of litter decomposition to N addition also varies among ecosystems; some studies in tropical forests showed a slower litter decomposition or soil

respiration rate under N addition (Mo et al., 2006; Fang et al., 2007; Zhang et al., 2020), mainly caused by a decreased microbial biomass (Chen et al., 2013; Li et al., 2014; Lu et al., 2021), slower enzyme activities (Carreiro et al., 2000; Xiao et al., 2018) and suppressed N mining (Berg and Matzner, 1997; Magill and Aber, 1998; Neff et al., 2002; Hagedorn et al., 2003). In summary, the conflicting results from different studies and the different response of soil C and litter C decomposition to N addition may be explained by the degree of N limitation in different ecosystems, the duration and magnitude of N deposition, and different characteristics of soil C and litter C.

Generally, tropical forests are P-limited ecosystems (Hou et al., 2020), and the dynamics of litter and soil C decomposition will respond to P addition to a greater extent than N addition (Cleveland and Townsend, 2006; Chen et al., 2016; Poeplau et al., 2017; Hui et al., 2020; Zhang et al., 2020). Considerable studies have shown that P addition in tropical forests could accelerate the decomposition of soil C (Liu et al., 2012; Mori et al., 2015; Hui et al., 2020) and litter (Cleveland et al., 2002; Jacobson and Bustamante, 2014; Chen et al., 2016), thus decreasing soil C stocks (Poeplau et al., 2016). Accelerated litter or soil C decomposition under P addition can be attributed to three complementary mechanisms: 1) Soil microbial community composition (Liu et al., 2012) was altered to favor the growth of microbes and production of C-degrading enzymes under P addition (Mori et al., 2018); 2) P addition may liberate microbes from P deficiency (Rousk and Baath, 2007; Cruz et al., 2009; Li et al., 2014), and thus stimulates litter and soil C decomposition (Hobbie and Vitousek, 2000; Mori et al., 2018); 3) Enhanced availability P plus the sufficient C sources may cause N limitation of microbial growth, and thus force microbes to acquire N through soil organic matter (SOM) mineralization (Mehnaz et al., 2019). However, the positive feedbacks between litter or soil C decomposition and P addition does not happen in all situations; a negative (Chen et al., 2013; Mori et al., 2015; Fang et al., 2019) or no response (McGroddy et al., 2004; Zhang et al., 2020) has also been found. Increased P availability will decrease “microbial P mining” during which labile C is used to decompose SOM for P hydrolysis in soils with low availability of inorganic P. This is associated with 1) down-regulated microbial investment in enzyme production (Wang et al., 2020); 2) unchanged (Turner and Wright, 2014; Chen et al., 2019) or decreased C-degrading enzyme activities (Chen et al., 2013; Jing et al., 2016); 3) altered microbial community composition (Fang et al., 2019).

The uncertain response of litter and soil C decomposition to N and P addition calls for further detailed studies to investigate underlying mechanisms. So far, most studies have focused on either litter (Chen et al., 2016; Averill and Waring, 2018; Zhang et al., 2020) or soil C (Fang et al., 2019; Tian et al., 2019) decomposition, while integrated field studies to simultaneously test litter and soil C decomposition are scarce (Sayer et al., 2011). Here, we used an 11-years long-term N and P addition experiment in a tropical forest in south China, combined with a natural abundance isotope study, so that we can quantify the effect of N and P addition on litter decomposition and soil C mineralization at the same time. We used dried corn leaves and corn roots (i.e. from a C_4 plant with a ^{13}C isotope composition different from that of forest soil C, which was derived from C_3 plants)

as litter input, which were mainly differed in lignin concentration. We mixed the litter with nutrient-addition soils to monitor leaf litter and SOC decomposition in a tropical forest. This site has low P and high N availability (Wang et al., 2014), therefore, we anticipated that N addition would impede the C turnover, whereas P addition would accelerate C turnover. Concretely, we hypothesized that: (H1) Total CO₂ release will be slowed by N addition but accelerated by P addition; (H2) Both of the litter and soil C decomposition will be impeded by N addition, but accelerated by P addition. (H3) Corn leaves will decompose faster than corn roots. To verify our hypotheses, total CO₂ efflux was measured and partitioned based on isotope composition, and we monitored changes in extracellular enzyme activities and microbial community composition every three months to investigate the underlying mechanism.

2. Material and methods

2.1. Soil collection

We collected soils from a 11-years nutrient addition experiment at the Xiaoliang Research Station of Tropical Coastal Ecosystems, Chinese Academy of Sciences (21°27'0"N, 110°54'0"E), Southwestern Guangdong Province, China. Descriptive information on this site and experimental design were given in Wang et al. (2014). Shortly, the soil was a latosol with a pH of c. 4 and low availability of P. In August 2009, a factorial nutrient addition experiment for N and P was established in a completely randomized block design. Within five replicate blocks, a control (CK), and treatments of N addition (+N), P addition (+P), and N and P addition (+NP) were randomly assigned to four 10 m × 10 m plots (Zhao et al., 2014). Starting in September 2009, the plots were fertilized to a total application of 100 kg N or P ha⁻¹ year⁻¹. We dissolved 476.6 g NH₄NO₃ (equal to 166.6 g N) and/or 808 g NaH₂PO₄ (equal to 166.6 g P) in 30 L groundwater and applied the solution to the corresponding blocks using a backpack sprayer every two months. For control plots, 30 L groundwater was added. The amounts of N and P added are equal to other N addition (Lu et al., 2010) and P addition (Liu et al., 2012) experiments in this region. In December 2019, we took eight soil cores to 0–5 and 5–10 cm depth at random in each plot and homogenized soils from each treatment into one soil sample. The soils were sieved (2-mm mesh) to remove stones and roots. The physiochemical properties of the soils are presented in Table 1.

2.2. Experimental design

To assess the effect of N and P availability on litter and soil C decomposition, a 12-months field decomposition experiment was conducted. Two types of litter were chosen: corn leaves and corn roots, which differs in chemical properties, especially in lignin content. The ¹³C isotopic abundance of corn leaves and corn roots was -14.4‰ and -15.2‰, respectively (Table S1), whereas the ¹³C isotopic abundance of soils from our site was c. -28‰ (Table 1). Moreover, the chemical characteristics of corn residues were in the range of the leaf litter and woody debris from our

site (Table S2). Considering the logistics of labeling field litters, we made a compromise and used corn residues to substitute field litters. Corn leaves or roots were mixed with 70 g dry weight equivalent of fresh soil from each treatment to double the organic C content in soils for three reasons: (1) the amount of corn residue added to soil was close to the actual litter input into the surface soil layers (0–5 cm, 16–18 g C kg⁻¹ soil yr⁻¹); (2) based on a previous incubation experiment using soil from this site, we added 4.4 mg C dry soil for a 90-days incubation experiment (Zhang et al., 2020); for the 12-months field experiment, we doubled the SOC content to investigate how litter and soil C changed over a longer time; (3) with the same amount of litter C input into soil, it was easier to compare with soil C decomposition. Therefore, we simply doubled the SOC content, rather than considering the annual litter input. The amount of the corn residues mixed with soils were given in Table S3. The mixtures were placed inside a 0.15 mm-mesh 10 cm × 15 cm nylon bag to prevent effects of soil animals and plant roots. We collected the samples every three months over one year, and the treatment included two types of litter addition, four nutrient additions and two soil layers. Thus, we prepared 320 bags in total (four sampling time × four nutrient addition treatments × two litter types × two soil depths × five replicate blocks). After the nylon bags were put into the place where the soil cores were collected, one nylon bag of each treatment from each block was collected every three months.

2.3. Gas analyses and soil sampling

The soil on the surface of nylon bags was removed gently, and the soil samples were then transferred to plastic sample bags for later analysis. Total CO₂ efflux was assessed by incubation and determined the source using the ¹³C isotope signature. Aliquots of 10 g dry-weight equivalent of fresh soils were transferred to 250 mL glass flasks, sealed with Parafilm and incubated at 25 °C in the dark for 24 h. After the incubation, the flasks were evacuated with CO₂-free air and resealed for four hours before sampling. After four hours, 200 mL gas in the flask was collected and diluted with 100 mL CO₂-free air, resulting in 300 mL gas samples for analysis of CO₂ concentrations and ¹³C isotopic abundance using a Cavity Ring-down Spectrometer (G2201-i Isotopic CO₂/CH₄, Picarro, Santa Clara, CA, USA).

2.4. Enzyme analysis

The activities of enzymes involved in the decomposition of cellulose (β-1,4-glucosidase; BG), and the degradation of lignin (phenol oxidase; PHO; and peroxidase; PER (Freeman et al., 2004; Ghafoor et al., 2017; Nannipieri et al., 2018) were assessed. BG was measured by adding the substrate *p*-nitrophenyl-phosphate tetrahydrate bound to the chromogen *p*-nitrophenol (pNP) (Tabatabai and Bremner, 1969), and incubating the samples at 37 °C for 1 h. After incubation, we quantified the released pNP at 405 nm spectrophotometrically (Multiskan™ FC, Thermo Fisher Scientific, Waltham, MA, USA). We use L-3,4-dihydroxyphenylalanine (DOPA) as substrate to measure Oxidative activities of PHO and PER spectrophotometrically according to Saiya-Cork et al. (2002).

Table 1

Physiochemical characteristics of soils from nutrient addition treatments in a secondary tropical forest, where CK is unfertilized controls, +N is nitrogen (N) addition, +P is phosphorus (P) addition, +NP is both N and P addition, and TN is total N concentration, TP is total P concentration, SOC is soil organic carbon concentration, NH₄⁺-N is ammonium-N concentration, NO₃⁻-N is nitrate N concentration, P_{extr} is extractable P concentration; values are means ± SE for n = 5; different lowercase letters within a column indicate significant differences among nutrient addition treatments at P < 0.05 (after correction for multiple comparisons).

Soil depths	Nutrient addition	TN (g kg ⁻¹)	TP (g kg ⁻¹)	SOC (%)	pH	NO ₃ ⁻ -N (mg kg ⁻¹)	NH ₄ ⁺ -N (mg kg ⁻¹)	P _{extr} (mg kg ⁻¹)	d ¹³ C (‰)
0–5 cm	CK	2.1 ± 0.45	0.22 ± 0.02b	2.5 ± 0.43	3.8 ± 0.09ab	10 ± 1.1b	3.2 ± 0.45	2.8 ± 0.46b	-28.7 ± 0.18
	+N	2.5 ± 0.31	0.24 ± 0.01b	2.9 ± 0.56	3.5 ± 0.10b	17 ± 1.7a	4.7 ± 0.71	2.8 ± 0.42b	-28.7 ± 0.19
	+P	1.7 ± 0.30	0.47 ± 0.04a	2.1 ± 0.45	4.1 ± 0.11a	11 ± 1.2b	2.7 ± 0.51	82.3 ± 9.66a	-28.2 ± 0.27
	+NP	2.6 ± 0.34	0.55 ± 0.04a	3.3 ± 0.36	3.8 ± 0.10ab	12 ± 1.0ab	5.1 ± 0.85	76.2 ± 17.57a	-28.0 ± 0.30
	CK	1.5 ± 0.22	0.23 ± 0.01b	1.6 ± 0.18	3.8 ± 0.06	6 ± 0.5ab	2.0 ± 0.44	1.1 ± 0.14b	-28.2 ± 0.24
5–10 cm	+N	1.5 ± 0.24	0.20 ± 0.01b	1.8 ± 0.20	3.6 ± 0.09	9 ± 1.2a	1.8 ± 0.35	1.5 ± 0.36b	-28.3 ± 0.40
	+P	1.4 ± 0.09	0.39 ± 0.02a	1.4 ± 0.21	4.1 ± 0.08	7 ± 0.9ab	1.8 ± 0.28	32.4 ± 5.49a	-28.5 ± 0.25
	+NP	1.6 ± 0.16	0.38 ± 0.03a	2.0 ± 0.22	3.9 ± 0.08	6 ± 0.6b	1.3 ± 0.30	28.1 ± 8.32a	-28.1 ± 0.19

2.5. Phospholipid fatty acids (PLFAs)

We analyzed phospholipid fatty acids (PLFAs) to determine soil microbial community structure and microbial biomass according to Bossio and Scow (1998). Peaks were determined by comparison with a 19:0 internal standard using gas chromatography (GC7890, Agilent, Santa Clara, CA, USA) and assigned following standard nomenclature (Tunlid et al., 1989). The biomass of single fatty acids was presented as nmol g^{-1} soil dry weight and calculated based on the concentration of the 19:0 internal standard. Fungi were calculated from PLFAs 18:2 ω 6c, 18:3 ω 3c and 16:1 ω 5c (Frostegard and Baath, 1996). Bacterial biomass was represented by PLFAs i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, 16:1 ω 7c, 18:1 ω 9c, 18:1 ω 7c 15:0 and 17:0 (Bossio et al., 2006). The total PLFAs biomass of the soil microbial community was presented as the sum of fungi, bacteria and PLFAs 14:0, 16:0, 17:1 ω 8c. We calculated the ratio of fungi to bacteria (F/B ratio) to indicate changes in microbial community structure (Bardgett et al., 1996; Frostegard and Baath, 1996).

2.6. Data analysis

The litter or soil C release was calculated from the differences between ^{13}C isotopic abundance of the soil and litters using a two-pool mixing model (Zhu et al., 2014):

$$C_{\text{soil}} = C_{\text{total}} \times \frac{\text{atom}\%^{13}\text{C}_{\text{litter}} - \text{atom}\%^{13}\text{C}_{\text{total}}}{\text{atom}\%^{13}\text{C}_{\text{litter}} - \text{atom}\%^{13}\text{C}_{\text{soil}}}$$

$$C_{\text{litter}} = C_{\text{total}} - C_{\text{soil}}$$

where C_{total} is total C release, C_{soil} and C_{litter} are soil and litter C release, respectively, $\text{atom}\%^{13}\text{C}_{\text{total}}$, $\text{atom}\%^{13}\text{C}_{\text{soil}}$ and $\text{atom}\%^{13}\text{C}_{\text{litter}}$ are $\text{atom}\%^{13}\text{C}$ values of C_{total} , soil and litter, respectively.

Cumulative total C, litter or soil C release after 12 months were calculated by the total area of the line chart of C-release rate. Total $\text{CO}_2\text{-C}$, litter $\text{CO}_2\text{-C}$ and soil $\text{CO}_2\text{-C}$ was used to represent total C release, litter decomposition, and soil C decomposition. All subsequent statistical analyses were carried out in R.4.0.5 for Mac (R Core Team, 2021).

One-way ANOVAs were used to analyze the effect of long-term nutrient addition on soil physicochemical properties, litter properties before the decomposition experiment ($n = 5$). Where the effects were significant, we conducted post hoc tests (Tukey's HSD) to compare individual treatments.

Linear mixed-effects models (LMEs) (*lmer* function in the *lme4* package (Bates et al., 2015)) were used to evaluate the effect of nutrient addition treatments, litter types and soil depths on total, litter or soil C-release rate. In the LMEs, Nutrient addition treatments, litter types and soil layers were set as fixed effects, and replicate blocks and sampling time were included as random effects. We determined the model fit by comparing full models with null models, and the Chi-square values and p -values of the model fit are given (Table S3). We used likelihood ratio tests and Satterthwaites approximation in the *lmerTest* package (Kuznetsova et al., 2017) to determine the significance of each term. Where the interactive effect of nutrient addition treatments and litter types was significant, the individual model was used to analyze the differences among substrate-addition treatments within each nutrient addition treatments. Two-way ANOVAs were used to test the effect of nutrient addition treatments and litter types on cumulative C release at the end of the experiment; whenever ANOVA yielded significant effects, Tukey's HSD test was performed to assess the differences between nutrient addition or litter types at $P < 0.05$.

The effects of nutrient addition, litter types and their interactions on soil enzyme activities and microbial community composition were also tested using LMEs where nutrient addition treatments, litter types and soil depths were set as fixed effects, and replicate blocks and sampling time were set as random effects. Full models were compared with null models to determine the model fit and the Chi-square values and p -values of the model fit are given (Tables S5 and S6). Where overall models were significant, treatment contrasts at each sampling time were assessed using the *pairs* function in the

emmeans package (Lenth, 2021). Significant results were presented at $P < 0.05$ and marginally significant trends at $P < 0.1$.

The correlation analysis among the C-release rate, microbial community composition and enzyme activities was conducted using the *rcorr* function in the *Hmisc* package (Harrell, 2021), and the results of the correlation test are given in Tables S7 and S8. Finally, to assess the direct and indirect linkages between nutrient addition, microbial community composition, enzyme activities and C-release rate, we used structural equation modeling (SEM) in the *lavaan* package (Rossee, 2012). The a priori conceptual model included all possible hypothesized paths between variables, and non-significant paths were dropped from subsequent models until the best model fit was achieved. In the final model, we included the N and P addition as influencing factors, a latent variable $\text{lignin}_{\text{enzymes}}$ measured by the PHO and PER activity, BG activities, total PLFAs and F/B ratio to present microbial community composition. The data from the last sampling time (December 2020) were used to conduct the SEM. The Chi-square (χ^2) test was used to evaluate the overall fit of the model, alongside root mean square error of approximation, comparative fit index (CFI), and the goodness of fit index (Schermelleh-Engel et al., 2003).

3. Results

3.1. Total, litter and soil C release

Total C-release rates varied significantly among nutrient addition treatments and soil layers, while litter types had no significant influence on them (Fig. 1). Total C-release rates increased during the first six months, with a peak in June 2020, and then decreased during the following six months. Total C-release rate was significantly accelerated by N addition but decreased by P addition ($P < 0.01$, Fig. 1a and b), in contrast with our hypothesis 1 (H1). The cumulative total C release presented similar patterns as the total C-release rate, showing that N addition enhanced the cumulative total C release, while P addition decreased it ($P < 0.05$, Fig. S1a and b). NP addition, however, showed no significant influence on the cumulative total C release, except at 0–5 cm soil depths with added corn leaves ($P < 0.05$, Fig. S1a and b). Thus, total C release was enhanced by N addition and suppressed by P addition and was greater at 0–5 cm soil depths.

Nutrient addition and soil depths had a significant influence on litter decomposition rate ($P < 0.05$, Fig. 1c and d). Nitrogen and NP addition accelerated litter decomposition rate, while P addition had no significant influence on it compared with unfertilized controls ($P < 0.05$, Fig. 1c and d). At 5–10 cm soil depths, corn leaves decomposed faster than corn roots, but this tendency was not significant when the data from 0 to 5 cm soil depths combined, thus we reject hypothesis 3 (H3). The cumulative C release from litter at 0–5 cm soil depths was enhanced by N addition ($P < 0.05$, Fig. S1c and d), while P and NP addition had no significant influence on it. Moreover, N and P addition had no significant influence on the total litter decomposition, while corn leaves decomposed more than corn roots at 5–10 cm soil depths.

Phosphorus addition significantly decreased the soil C decomposition rate ($P < 0.01$, Fig. 1c, d), but neither N nor NP addition had significant influence on it, in contrast with our hypothesis 2 (H2). Soil depth and litter types had no significant influence on soil C decomposition rate. Cumulative soil C release was greater under N or P addition at 5–10 cm soil depths when we added corn leaves ($P < 0.05$, Fig. S1c and d), while there were no other noticeable differences caused by litter or nutrient addition. Hence, only P addition negatively influenced the soil C decomposition.

The decreased total C release under P addition soil was mainly caused by the decreased soil C decomposition, with the litter decomposition being unchanged. The enhanced total C release under N addition soil was accounted for by increased litter decomposition, while the soil C decomposition remained unchanged. Thus, N and P addition modified C release from litter and soil in different ways.

3.2. Enzyme activities

Nitrogen addition significantly enhanced BG activity, while P addition decreased it ($P < 0.001$, Fig. 2a). However, NP addition had no significant

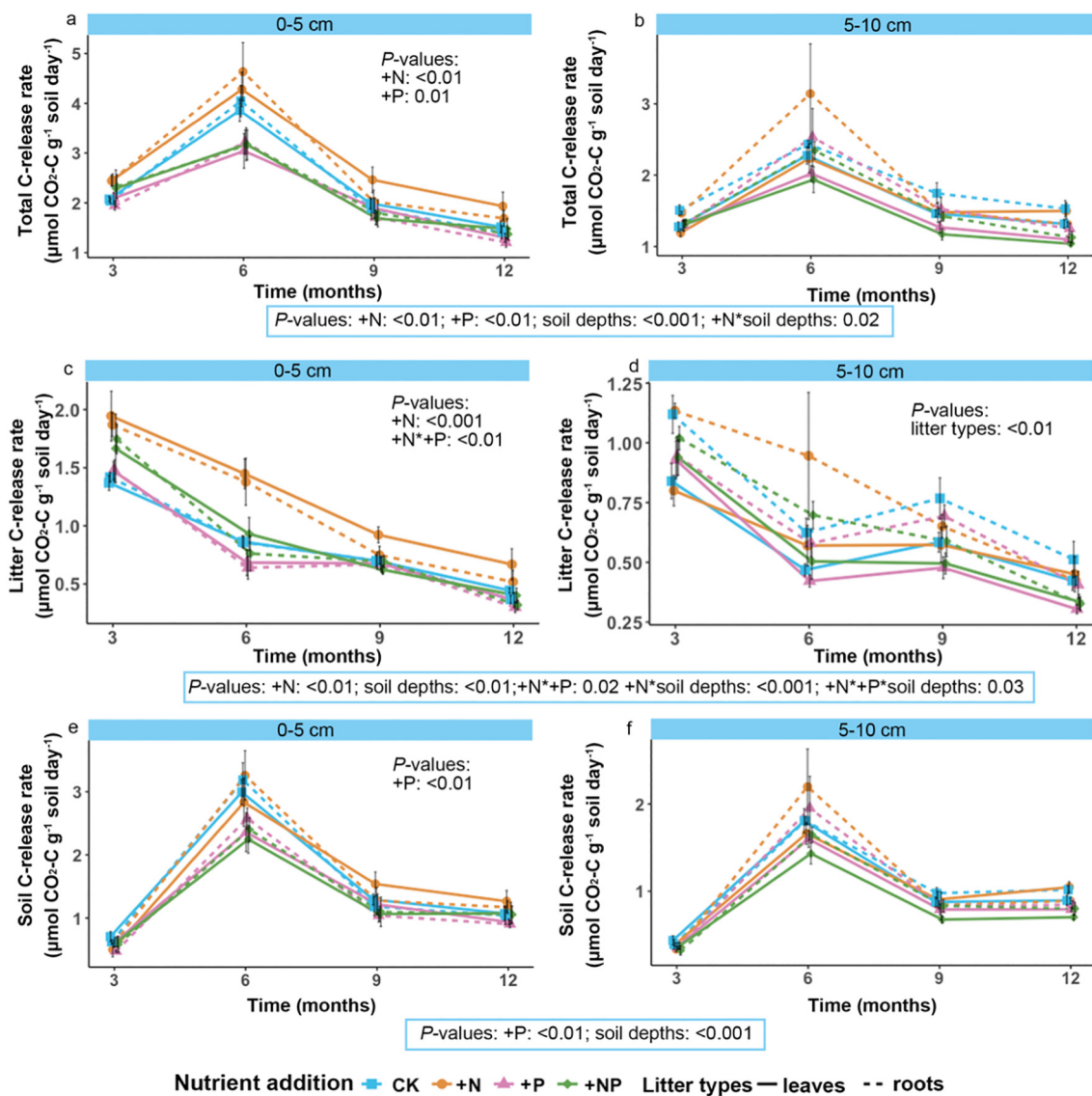


Fig. 1. Carbon (C)-release rates in soils from nutrient addition treatments during a 12-months field decomposition experiment in a secondary forest in south China, showing total C release at 0–5 cm (a) and 5–10 cm soil depths (b), litter C release at 0–5 cm (c) and 0–5 cm soil depths (d), soil C release at 0–5 cm (e) and 5–10 cm soil depths (f); CK (turquoise) is unfertilized controls, +N (orange) is nitrogen (N) addition, +P (hot pink) is phosphorus (P) addition, and +NP (green) is both N and P addition. Symbols and error bars represent means and standard errors for $n = 5$; P -values from linear mixed-effects models (LMEs) shown in each subfigure represent the effects of litter types and nutrient addition treatments at each soil depth and P -values from LMEs shown under each row represent the effect of litter types and nutrient addition treatments across all soil depths.

influence on BG activities; this may result from the additive effect of NP addition. BG activities were greater at 0–5 cm soil depths ($P < 0.05$, Fig. 2a). In general, no noticeable difference in BG activity was observed between different litter types, except for some certain sampling time (September 2020 and December 2020).

The dynamics of the PHO and PER activities showed a similar pattern as BG activities. There was no significant effect of litter type on PHO and PER activities, while they were higher at 0–5 cm soil depths than at 5–10 cm soil depths ($P < 0.05$, Fig. 2b and c). There was no obvious influence of separate N and P addition on PHO and PER activities, while NP addition significantly enhanced both of them ($P < 0.05$, Fig. 2b and c).

3.3. Microbial community composition

Nitrogen and P addition exerted different influences on the relative fungal abundance showing that N addition significantly increased the relative fungal abundance, while P addition had no influence on it compared with the unfertilized control ($P < 0.01$, Fig. 3a). There was no significant

influence of litter type on the relative fungal abundance ($P > 0.05$, Fig. 3a). The relative fungal abundance was greater at 5–10 cm than 0–5 cm soil depths ($P < 0.001$).

The relative bacterial abundance was reduced by N addition but enhanced by P and NP addition ($P < 0.01$, Fig. 3b). Moreover, the relative bacterial abundance was greater in soils added with corn roots than corn leaves ($P < 0.001$, Fig. 3b). There were no significant differences in the relative bacterial abundance between soil depths ($P > 0.05$, Fig. 3b).

The total PLFAs biomass was significantly enhanced by N addition but decreased by P addition ($P < 0.01$, Fig. 4a), while it was not influenced by NP addition. At 0–5 cm soil depths, the total PLFAs biomass was greater than that at 5–10 cm soil depths ($P < 0.05$, Fig. 4a). There were no significant differences in the total PLFAs biomass between soils supplied with corn leaves or corn roots.

The F/B ratio was greater in N-addition soils, and lower in P-addition compared with unfertilized controls ($P < 0.001$, Fig. 4b). The enhanced F/B ratio under N addition resulted from the increased relative fungal abundance and decreased the relative bacterial abundance, and we found the

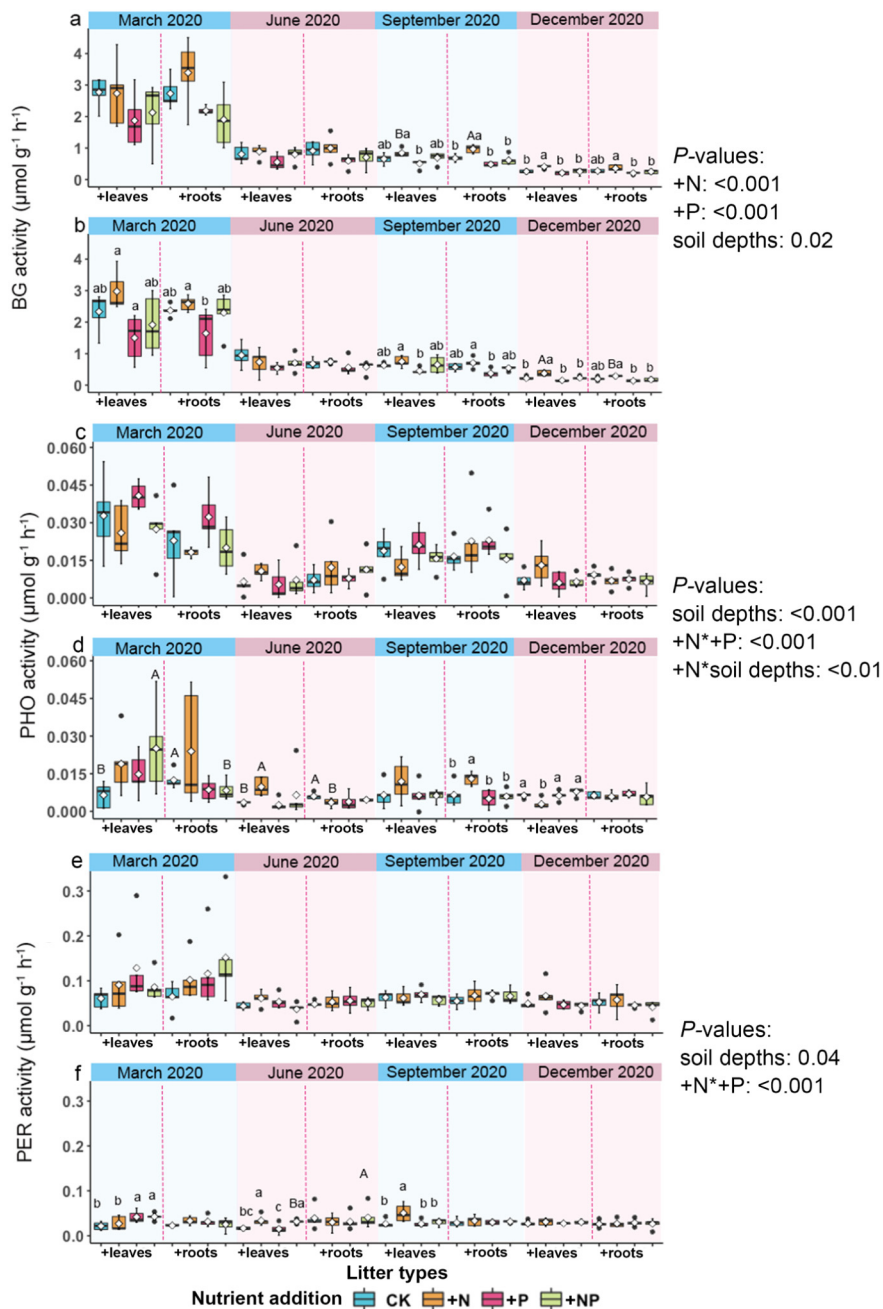


Fig. 2. Enzyme activities in soils from nutrient addition treatments during a 12-months field decomposition experiment in a secondary forest in south China, showing: β -1,4-glucosidase (BG) activities at 0–5 cm (a) and 5–10 cm (b) soil depths, phenol oxidase (PHO) activities at 0–5 cm (c) and 5–10 cm (d) soil depths and peroxidase (PER) activities at 0–5 cm (e) and 5–10 cm (f) soil depths at each sampling time, where CK (turquoise) is unfertilized controls, +N (orange) is nitrogen (N) addition, +P (hot pink) is phosphorus (P) addition, and +NP (green) is both N and P addition. Different capital letters indicate significant differences between litter types and different lowercase letters indicate significant differences among nutrient addition treatments at $P < 0.05$ (after correction for multiple comparisons). P -values from linear mixed-effects models (LMEs) shown at the right of the figure represent the effects of nutrient addition, litter types, soil depths and their interactions.

opposite in P-addition soils. The F/B ratio was greater at 5–10 cm soil depths than at 0–5 cm soil depths ($P < 0.05$). Also, the F/B ratio was greater in soils added with corn roots than corn leaves ($P < 0.05$, Fig. 4c).

Generally, N and P addition exerted opposite influences on microbial community composition, showing that N addition increased the relative fungal abundance and decreased the relative bacterial abundance, while P addition had no significant influence on the relative fungal abundance increased the relative bacterial abundance. Nitrogen addition enhanced both the total PLFAs biomass and F/B ratio, while P decreased both.

3.4. Correlations among the C-release rate and microbial activities

In the first three months, the C-release rate (total, litter and soil C-release rate) had strong positive correlations with PHO, PER and total PLFAs biomass, while negative correlations were observed among the relative fungal abundance, F/B ratio and C-release rate ($P < 0.05$, Fig. 5 and Table S7). After three months of decomposition, correlations between C-release rate and relative fungal and bacterial abundance was weaker. Strong correlations were found among C-release rate, enzyme activities and the total PLFAs biomass ($P < 0.01$, Fig. 5 and Table S7). The

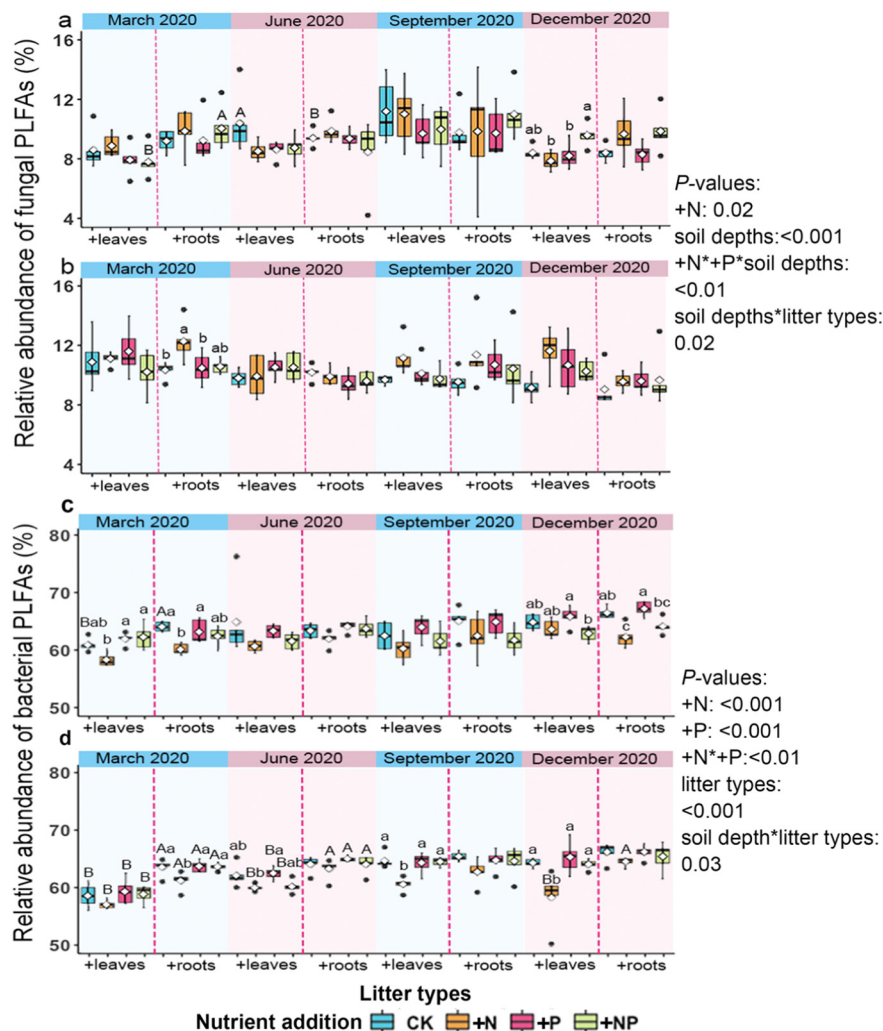


Fig. 3. The relative abundance of fungal and bacterial abundance in soils from long-term fertilization treatments during a 12-months field decomposition experiment in a secondary forest in south China, showing: relative fungal abundance at 0–5 cm (a) and 5–10 cm (b) soil depths and relative bacterial abundance at 0–5 cm (c) and 5–10 cm (d) soil depths at each sampling time. Abbreviations, statistical significance and *P*-values follow the legend to Fig. 2.

correlations among the C-release rate, enzyme activities and microbial community composition were more intense at 0–5 cm soil depths than at 5–10 cm soil depths (Fig. S2 and Table S8).

3.5. Structural equation modeling (SEM)

We used structural equation modeling (SEM) to determine the direct and indirect pathways mediating C release. There was a total positive effect of N addition on C-release rates, while P addition had a negative effect on them (Fig. 6). The magnitude of the effect of P addition on C release was greater than that of N addition (Fig. 6b, d and f). Moreover, the influence of N and P addition on C-release rate was mainly through direct pathways. Nitrogen addition also increased total PLFAs, F/B ratio and lignin_{enzymes} and BG activities, thus indirectly enhanced C-release rate. Phosphorus addition, however, inhibited C release indirectly through decreasing total PLFAs biomass, F/B ratio and lignin_{enzymes} and BG activities. In general, the enhanced lignin_{enzymes} and total PLFAs biomass favors the C release, while the increased F/B ratio and BG activities associated with the decreased C-release rate, but not significantly.

4. Discussion

Our study provides insight into how soil N and P availability affect the litter and soil decomposition and the underlying microbial mechanisms.

First, N addition enhanced total C release by increasing litter decomposition, while it had no influence on the soil C decomposition. On the other hand, P addition decreased total C release via impeding soil C decomposition without altering litter decomposition (H1 and H2). Finally, although corn leaves and corn roots had different chemical properties, there were no significant differences in the decomposition rate and the magnitude of their influences on the soil C decomposition rate (H3). Though the findings contradict with all our hypothesis and disagree with several studies conducted in tropical forests (Mo et al., 2006; Fang et al., 2007; Zhang et al., 2020), changes in C-degrading enzyme activities, microbial biomass and F/B ratio under N or P addition could support our findings.

4.1. Litter decomposition

Different from our hypothesis 3 (H3), there were no significant differences between the decomposition rate of corn leaves and corn roots. Decay rates are commonly inversely related to cellulose and lignin concentration of the substrate and positively related to N and P concentrations (Berg and McClaugherty, 2003; Cornwell et al., 2008; Michael et al., 2009). The corn leaves had a higher N concentration, while the corn roots had a higher concentration of P, cellulose and lignin. We surmise that higher litter P concentration may offset the negative influence of the greater cellulose and lignin concentration. Thus, the litter P concentration might be a key factor affecting the litter decomposition process, especially

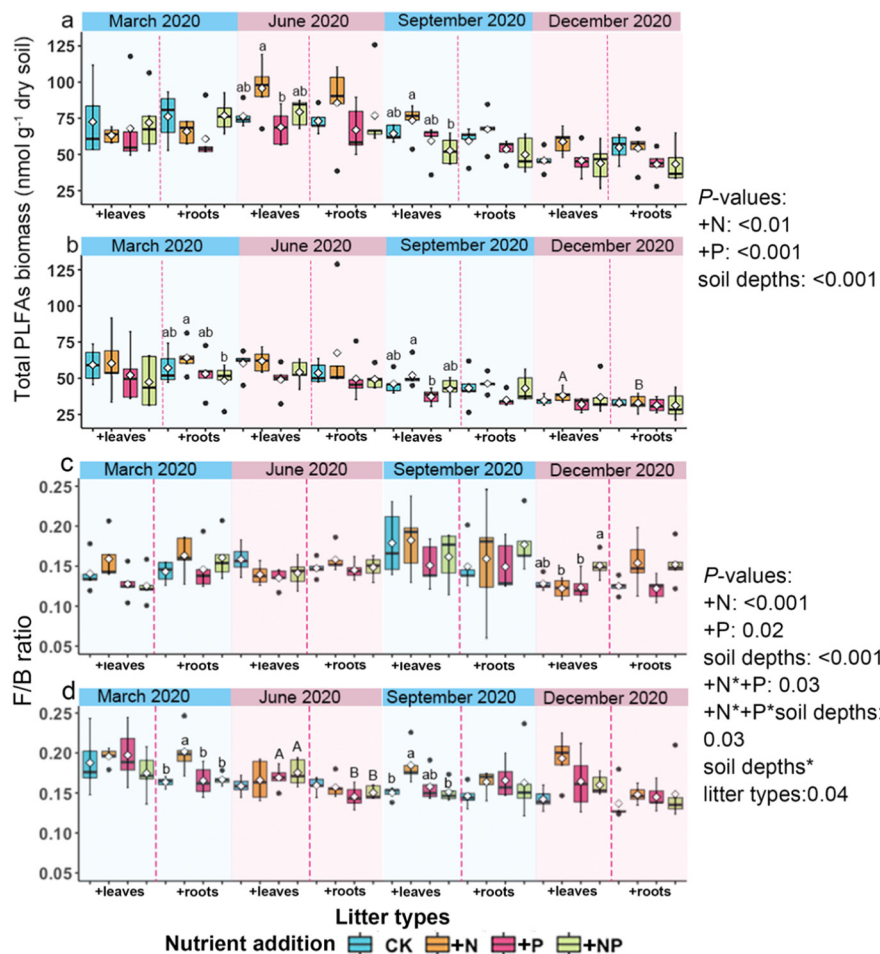


Fig. 4. The total PLFAs biomass and F/B ratio in soils from nutrient addition treatments during a 12-months field decomposition experiment in a secondary forest in south China, showing: total PLFAs biomass at 0–5 (a) and 5–10 cm (b) soil depths and F/B ratio at 0–5 (c) and 5–10 cm (d) soil depths at each sampling time. Abbreviations, statistical significance and *P*-values follow the legend to Fig. 2.

in P-deficient tropical forest soils (Wang et al., 2014) which agrees with previous findings at this site (Chen et al., 2016; Zhang et al., 2020).

Nitrogen addition enhanced the litter decomposition rate, which does not support our hypothesis 2 (H2) and previous findings in tropical forests that N addition inhibited litter decomposition (Fang et al., 2007; Mo et al., 2008; Zhou et al., 2017; Zhang et al., 2020). However, considering enzyme activities and microbial community compositions, our findings can be well explained. First, stimulated BG activities under N addition facilitated litter decomposition, because BG was the main extracellular enzymes decomposing cellulose (Ghafoor et al., 2017). Second, the enhanced relative fungal abundance in N-addition soils indicated that fungi played a critical role in litter decomposition, especially when substrate had a relatively high cellulose and lignin content (Aneja et al., 2006; Rousk and Baath, 2007; Kuramae et al., 2013; Talbot et al., 2013). Moreover, greater F/B ratios were also observed under N addition, which was in line with previous findings that increased fungal biomass and F/B ratio may promote decomposition of recalcitrant components in substrates (Kuzakov, 2010; Fontaine et al., 2011). Third, although there were no significant changes in PHO and PER activities under N addition, N addition exerted a positive influence on PHO and PER activities through increasing the F/B ratio according to the correlation and SEM results since the PHO and PER activities are generally related to fungi (Sinsabaugh, 2010). The main function of phenol oxidases was to reduce oxygen to hydrogen peroxide (H₂O₂) and catalyze the degradation of polysaccharides and lignin (Sinsabaugh, 2010). Thus, N addition might indirectly alter PHO and PER activities and enhance litter decomposition. Finally, soil microbial processes in tropical forests under long-term nutrient addition are generally C limited

(Eberwein et al., 2015), and the addition of plant-derived C thus might liberate soil microbes from C limitation, in accordance with increased enzyme activities and microbial biomass in the present study and other findings in tropical forests (Qiu et al., 2016; Fan et al., 2019a). Therefore, N addition enhanced microbial activities and mediated litter decomposition.

The overall lack of stimulation of litter decomposition under P addition in this study did not verify our hypothesis 2 (H2) and contradicts other studies conducted in tropical forests (Cleveland et al., 2002; Jacobson and Bustamante, 2014; Chen et al., 2016); however, it was in line with a previous study at this site (Zhang et al., 2020). BG activities decreased significantly in P-addition soils which would decrease cellulose decomposition (Ghafoor et al., 2017). Previous studies in tropical forests discovered that microbes down-regulate investments in enzyme release when P is sufficient (Yao et al., 2018; Wang et al., 2020), which supports our findings. However, there was an increase in the relative bacterial abundance in soils supplied with P. Bacteria can also benefit from readily-available substances formed during degradation of complex macromolecules by fungal exoenzymes (De Boer et al., 2005; Romani et al., 2006) which may neutralize the negative effect of decreased enzyme activities and also explain the unchanged litter decomposition under P addition. Although there was no significant influence of P addition on the litter decomposition, our SEM result showed a sign of negative influence brought by P addition on litter decomposition through decreased PHO and PER activities, total PLFAs biomass and F/B ratio. Moreover, under NP addition, the litter decomposition rate was also increased, albeit it less than under N addition, showing the additive effect of N and P. When supplies of C, N and P simultaneously meet microbial demands, decomposition rate peaks (Melillo et al., 1982; Sterner



Fig. 5. Pearson rank correlation between total, litter or soil carbon (C)-release rate, enzyme activities, microbial community composition across all soil depths from nutrient addition treatments during a 12-months field decomposition experiment in a secondary forest in south China after each sampling time. BG is the β -1,4-glucosidase activity, PHO is the phenol oxidase activity and PER is the peroxidase activity. Circles with red and blue colors indicate positive and negative correlations, respectively; circle size indicates the *P*-values and *, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001.

and Elser, 2002), while excessive P may lead to a decrease in enzyme production (Yao et al., 2018; Wang et al., 2020). Therefore, NP addition can also stimulate litter decomposition, but to a smaller extent than N addition alone.

4.2. Soil C decomposition

Nitrogen addition had no significant influence on soil C decomposition, while P addition inhibited it, thus we reject our hypothesis 2 (H2). How soil C decomposition responds to N and P addition is different from the response of litter C, showing selectively modifications of N and P on these two different C sources. Although the total amount of litter C and soil C were set to the same, the physiochemical characteristic played an important role in their decomposition in response to N and P addition. Apart from C, litters contain more nutrients (such as N, P and other mineral elements) than soils, making them more accessible to microbes (Aerts, 1997). Conversely, the composition of soils is more complex, with the particulate C the easiest to decompose (Cotrufo et al., 2019) and the mineral-associated C more persistent in soils through chemical bonding to minerals and physical protection in small aggregates (Koegel-Knabner et al., 2008).

Studies conducted in tropical forests showed a decreased soil C release (Mo et al., 2008; Hui et al., 2020) and enhanced soil C sequestration (Lu et al., 2021) under N addition. However, a meta-analysis showed N addition had no influence on soil C decomposition in tropical forests (Liu and Greaver, 2010), but some experimental studies showed an enhanced soil C decomposition in tropical forests under N addition (Cleveland and Townsend, 2006; Fan et al., 2019b). Though the findings did not support our hypothesis, clues could be found in microbial activities and previous studies conducted in this site. First, although there was an increase in the relative fungal abundance and BG activities, the relative bacterial abundance was lower in N-addition soils which was in line with our previous study at this site (Li et al., 2014). Fungi are generally the principal agents in degradation of recalcitrant organic matter (Sinsabaugh, 2010), while bacteria are effective in degradation of labile organic matter and utilize the readily-available substances formed during degradation of complex macromolecules by fungal exoenzymes (De Boer et al., 2005; Romani et al., 2006). Thus, without the help of bacteria, the following degrading process might be impeded and influence the soil C degrading. Second, previous studies showed that N addition accelerates decomposition of labile soil C, while it inhibited decomposition of recalcitrant soil C (Neff et al., 2002; Janssens et al., 2010) which was partly in line with our findings and explains why N addition enhanced the litter C decomposition while had no significant influence on soil C decomposition. Chen et al. (2020) found that N addition enhanced the accumulation of mineral-associated organic C (MAOC), which is closely associated with the mineral surface and considered recalcitrant SOC (Rowley et al., 2018; Lavalley et al., 2020). We thus speculate that the insignificant effect of N on soil C decomposition might be caused by enhanced particulate organic C (POC) decomposition and accumulation of MAOC (Lu et al., 2021). Thus, the unchanged soil C decomposition under N addition might be explained by a combined effect of enzyme activities, microbial community composition and physical protections of soil C.

The soil C decomposition was inhibited by P addition which led to rejection of our hypothesis 2 (H2). Under most conditions, P addition is supposed to enhance the soil C decomposition in tropical forests (Hobbie and Vitousek, 2000; Mori et al., 2018), since P limits productivity and greater P availability could relieve degrading microbes from P limitation (Rousk and Baath, 2007; Cruz et al., 2009; Li et al., 2014). However, there is also a decreased soil C decomposition under P addition in some tropical forests (Chen et al., 2013; Fang et al., 2019), similar as in the present study. We interpreted our findings with microbial activities combined with previous studies conducted in this site. First, though there was an increase in the relative bacterial abundance, bacteria alone cannot degrade the complex macromolecules without involvement of fungi to produce oxidases, especially when microbes down-regulate investment in enzyme release (De Boer et al., 2005; Romani et al., 2006; Sinsabaugh, 2010). Moreover, some studies have found that "P mining" occurs in tropical forests (Chen et al., 2013; Zheng et al., 2015; Fang et al., 2019). Under P deficiency, microbes likely produce cellulases to degrade SOM and liberate organic P, therefore increasing P availability (Camenzind et al., 2018). Conversely, when P is sufficient, the addition of inorganic P might in turn decrease microbial investment in C-degrading enzymes, thus impeding soil C decomposition (Zheng et al., 2015). Second, although not statistically significant, P-addition soils had a lower SOC content than unfertilized controls before the decomposition experiment started (Table 1), similar as in other studies conducted in tropical forests which showed that short-term P addition depleted SOC storage (Cleveland and Townsend, 2006; Bradford et al., 2008; Poeplau et al., 2016). In P-addition soils, enhanced soil microbial activities degraded the labile C fraction at the early stage of nutrient addition, with the remaining C being more recalcitrant (Fang et al., 2019). The depleted SOC content under P addition might also explain why the increased litter decomposition rate was observed in this site at the early stage of P addition (Chen et al., 2016), while unchanged litter decomposition (Zhang et al., 2020) or decreased soil C decomposition (Zhang et al., 2021) were observed in more recent studies. Therefore, we assume that the influence of P on soil C decomposition depends on the duration of P addition, since

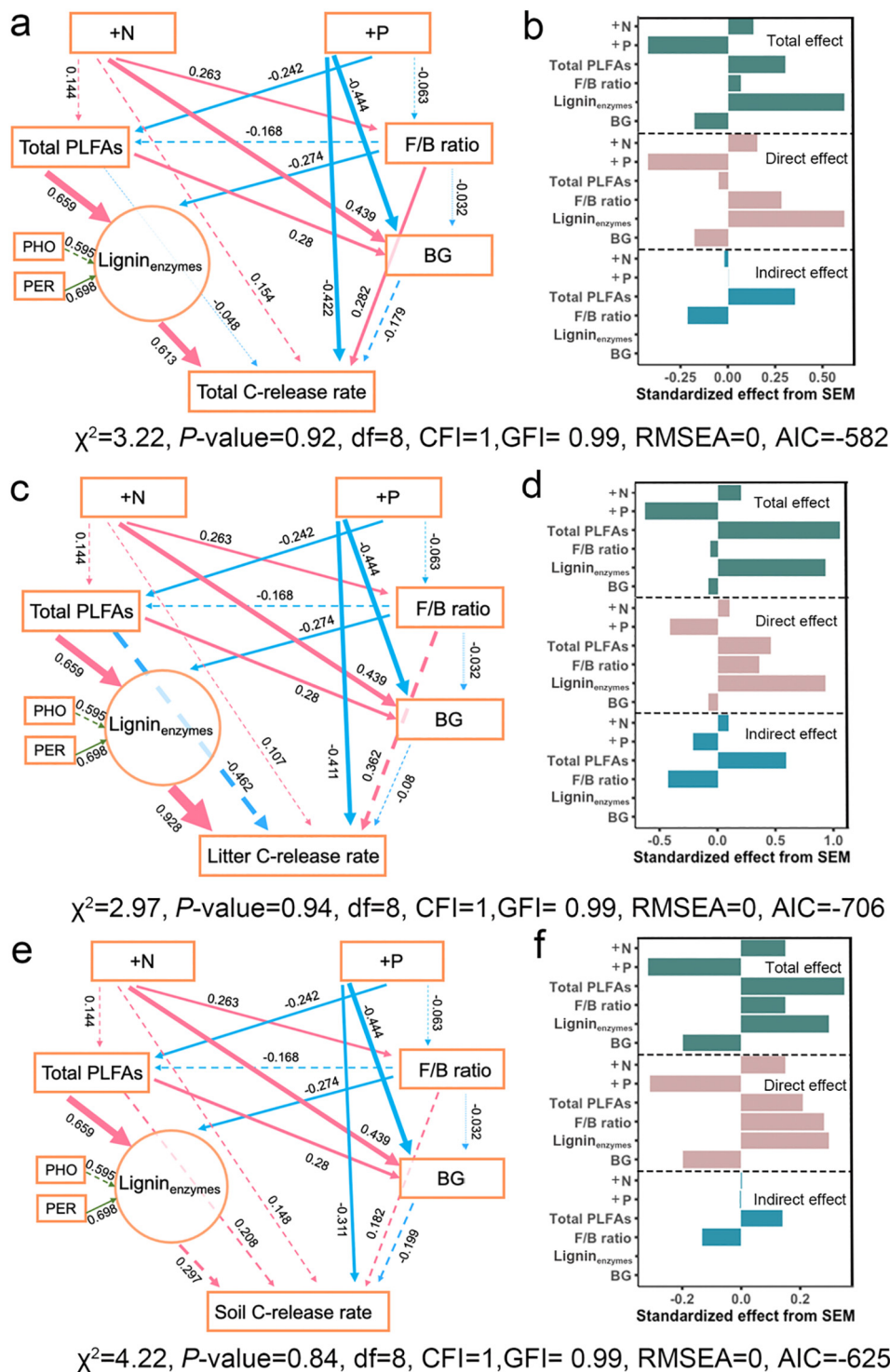


Fig. 6. Structural equation modeling (SEM) indicating how soil and microbial properties affect the total (a), litter (c) and soil (e) C-release rate at the end (December 2020) of a 12-months field decomposition experiment in a secondary tropical forest in south China. In panel (a), (c) and (e), lignin_{enzymes} is a latent variable measured by PHO and PER, BG is β -1,4-glucosidase activities; dashed or solid green arrows indicate the first and second measurement variables, respectively, and numbers parallel to arrows represents standardized loads. Solid red and blue arrows indicate significant positive and negative correlations, respectively ($P < 0.05$), and dashed red and blue arrows indicate insignificant positive and negative trends, respectively. Numbers parallel to arrows represent standardized path coefficients, the magnitudes of which are proportional to the thickness of arrows. In panel (b), (d) and (f), the total effect is the sum of direct and indirect effects; χ^2 , chi-square; df, degrees of freedom; CFI, comparative fit index; GFI, goodness-of-fit index; RMSEA, root mean square error of approximation; AIC, Akaike's information criteria, $n = 80$.

long-term P addition could modify the SOC storage along with microbial activities. Finally, based on the balance of N and P requirements of microbes, P addition to N-sufficient tropical forests may also lead to reduced “P mining” (Elser et al., 2007; Vitousek et al., 2010), since that balance was

reached. This is evidenced by the result that NP addition had no significant influence on soil C decomposition because there were sufficient nutrients for microbial growth, but microbes reduced their capacity for “P mining” and thus their ability to degrade organic matter (Zheng et al., 2015).

4.3. Limitations of the present study

The field incubation experiment was intended to assess difference in litter (new C) and soil organic matter (old C) decomposition in response to N and P addition in a tropical forest. We acknowledge that the field incubation study had some limitations for understanding of SOC and litter decomposition in a tropical forest. First, the addition of corn residues, rather than litter from the field, might introduce some uncertainties considering different litter quality. However, in this study, there was no corn residue type effect (corn leaves vs corn roots) on litter or soil C decomposition, suggesting that litter quality was not a significant factor in this study. However, we suggest that isotope-labeled forest litter would be a more effective method to conduct similar experiments in the future, because this can avoid the effect of litter quality on the decomposition process. Second, the added litter quantity might also induce some uncertainties. In this study, the amount of corn residue added to soil was similar to the actual litter input into the surface soil layers (0–5 cm, 16–18 g C kg⁻¹ soil yr⁻¹). During litter decomposition, the N and P in the added litter will be released into soil, leading to the amount of N or P applied to soil or utilized by microbes being greater than the added mineral N or P. Therefore, when investigating litter decomposition under nutrient addition, the amount of nutrients released from litter should also be monitored and be taken into consideration when interpreting the results. However, in this study, we also added the same amount of litter in the control plots which would eliminate the effect of litter quantity, because all treatments received similar amounts of litter. Third, this study, which was conducted in the field, only measured C emission four times a year, and thus might miss any peaks of decomposition and thus bias the findings. Different from lab incubation experiment, where C emission can be measured multiple times, each field sampling in this study was destructive. The three-months intervals thus may have missed possible peaks of litter C decomposition, because this generally increases soon after addition. However, the aims of this study were to assess differences between litter (new C) and soil organic matter (old C) decomposition in response to N and P addition. Although the short-term response is important to understand mechanisms, litter decomposition is a long-term process, and usually lasts for years, even in tropical forests. The current experimental design thus can still address our key questions. In this study, we cannot exclude all the above-mentioned uncertainties, but the present study did provide new insights on litter and soil organic C decomposition under different N and P availability. We also explained underlying mechanisms.

5. Conclusions

The present findings demonstrate that N and P addition exerted opposite influences on litter and soil C release, showing that N addition enhanced litter decomposition, while P addition inhibited soil C decomposition. The distinct changes in C release from litter and soil under N and P addition can be ascribed to variation in enzyme activities and microbial community compositions. Moreover, there were no significant differences between the decomposition of corn leaves and roots, indicating that, besides the litter lignin and cellulose content, the P concentration should be taken into consideration for future soil C modeling, since productivity in tropical forests is usually P limited. Our study suggests that experiments that only test how N and P availability influence soil C release may not reflect the actual response of certain process of organic C decomposition, since litter and SOC decomposition were differently altered by soil N and P availability. The current findings indicate that microbes may not be limited by P in P-deficient soils, because “P mining” was also observed in this study. The imbalanced N and P availability in tropical forests may lead to the selective decomposition of litter or soil C, especially when suffering from increasing atmospheric N deposition. Our study further implies that the increased or decreased soil C release may result from different mechanisms and the seemingly unchanged soil C storage may undergo shifts between litter and soil C decomposition, which may alter the soil C stability under future climate change.

CRediT authorship contribution statement

Jingfan Zhang, Jingge Zhou, Yingwen Li, Guoming Qin and Yongxing Li performed the experiments. Jingfan Zhang analyzed the data. Jingfan Zhang, Hans Lambers and Faming Wang wrote this manuscript. All co-authors revised the manuscript.

Declaration of competing interest

None declared.

Acknowledgements

This study was funded by the National Natural Science Foundation of China (31870463, 32011530164, 31670621, 32171594, U2106209), the Key Special Project for Introduced Talents Team of Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou) (GML2019ZD0408), the Guangdong Basic and Applied Basic Research Foundation (2021B1515020011), the CAS Youth Innovation Promotion Association (2021347), the National Forestry and Grassland Administration Youth Talent Support Program (2020BJ003), and the R & D program of Guangdong Provincial Department of Science and Technology (2018B030324003).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.155049>.

References

- Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79, 439–449. <https://doi.org/10.2307/3546886>.
- Aneja, M.K., Sharma, S., Fleischmann, F., Stich, S., Heller, W., Bahnweg, G., Munch, J.C., Schloter, M., 2006. Microbial colonization of beech and spruce litter - influence of decomposition site and plant litter species on the diversity of microbial community. *Microb. Ecol.* 52, 127–135. <https://doi.org/10.1007/s00248-006-9006-3>.
- Averill, C., Waring, B., 2018. Nitrogen limitation of decomposition and decay: how can it occur? *Glob. Chang. Biol.* 24, 1417–1427. <https://doi.org/10.1111/gcb.13980>.
- Bardgett, R.D., Hobbs, P.J., Frostegard, A., 1996. Changes in soil fungal:bacterial biomass ratios following reductions in the intensity of management of an upland grassland. *Biol. Fertil. Soils* 22, 261–264. <https://doi.org/10.1007/BF00382522>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *Stat. Comput.* 067, 133–199. <https://doi.org/10.1007/s00248-015-0000-4>.
- Berg, B., Matzner, E., 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. *Environ. Rev.* 5, 1–25.
- Berg, B., McLaugherty, C., 2003. *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration*. Springer-Verlag, Berlin Heidelberg, pp. 11–15.
- Berg, B., Davey, M.P., De Marco, A., Emmett, B., Fauri, M., Hobbie, S.E., Johansson, M.B., Liu, C., McLaugherty, C., Norell, L., Rutigliano, F.A., Vesterdal, L., De Santo, A.V., 2010. Factors influencing limit values for pine needle litter decomposition: a synthesis for boreal and temperate pine forest systems. *Biogeochemistry* 100, 57–73. <https://doi.org/10.1007/s10533-009-9404-y>.
- Bossio, D.A., Scow, K.M., 1998. Impacts of carbon and flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. *Microb. Ecol.* 35, 265–278. <https://doi.org/10.1007/s002489900082>.
- Bossio, D.A., Fleck, J.A., Scow, K.M., Fujii, R., 2006. Alteration of soil microbial communities and water quality in restored wetlands. *Soil Biol. Biochem.* 38, 1223–1233. <https://doi.org/10.1016/j.soilbio.2005.09.027>.
- Bradford, M.A., Fierer, N., Reynolds, J.F., 2008. Soil carbon stocks in experimental mesocosms are dependent on the rate of labile carbon, nitrogen and phosphorus inputs to soils. *Funct. Ecol.* 22, 964–974. <https://doi.org/10.1111/j.1365-2435.2008.01404.x>.
- Bragazza, L., Buttler, A., Habermacher, J., Brancaleoni, L., Gerdol, R., Fritze, H., Hanajik, P., Laiho, R., Johnson, D., 2012. High nitrogen deposition alters the decomposition of bog plant litter and reduces carbon accumulation. *Glob. Chang. Biol.* 18, 1163–1172. <https://doi.org/10.1111/j.1365-2486.2011.02585.x>.
- Camenzind, T., Haettenschwiler, S., Treseder, K.K., Lehmann, A., Rillig, M.C., 2018. Nutrient limitation of soil microbial processes in tropical forests. *Ecol. Monogr.* 88, 4–21. <https://doi.org/10.1002/ecm.1279>.
- Carreiro, M.M., Sinsabaugh, R.L., Repert, D.A., Parkhurst, D.F., 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. *Ecology* 81, 2359–2365. <https://doi.org/10.2307/177459>.
- Chen, J.M., 2021. Carbon neutrality: toward a sustainable future. *The Innovation* 2, 100127. <https://doi.org/10.1016/j.xinn.2021.100127>.

- Chen, H., Dong, S., Liu, L., Ma, C., Zhang, T., Zhu, X., Mo, J., 2013. Effects of experimental nitrogen and phosphorus addition on litter decomposition in an old-growth tropical forest. *Plos One* 8, e84101. <https://doi.org/10.1371/journal.pone.0084101>.
- Chen, Y., Sayer, E.J., Li, Z., Mo, Q., Li, Y., Ding, Y., Wang, J., Lu, X., Tang, J., Wang, F., 2016. Nutrient limitation of woody debris decomposition in a tropical forest: contrasting effects of N and P addition. *Funct. Ecol.* 30, 295–304. <https://doi.org/10.1111/1365-2435.12471>.
- Chen, X., Hao, B., Jing, X., He, J.-S., Ma, W., Zhu, B., 2019. Minor responses of soil microbial biomass, community structure and enzyme activities to nitrogen and phosphorus addition in three grassland ecosystems. *Plant Soil* 444, 21–37. <https://doi.org/10.1016/j.scitotenv.2020.141318>.
- Chen, J., Ji, C., Fang, J., He, H., Zhu, B., 2020. Dynamics of microbial residues control the responses of mineral-associated soil organic carbon to N addition in two temperate forests. *Sci. Total Environ.* 748, 141318. <https://doi.org/10.1016/j.scitotenv.2020.141318>.
- Cleveland, C.C., Townsend, A.R., 2006. Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. *Proc. Natl. Acad. Sci. U. S. A.* 103, 10316–10321. <https://doi.org/10.1073/pnas.0600989103>.
- Cleveland, C.C., Townsend, A.R., Schmidt, S.K., 2002. Phosphorus limitation of microbial processes in moist tropical forests: evidence from short-term laboratory incubations and field studies. *Ecosystems* 5, 680–691. <https://doi.org/10.1007/s10021-002-0202-9>.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Perez-Harguindeguy, N., Queded, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Diaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Victoria Vaineretti, M., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes world-wide. *Ecol. Lett.* 11, 1065–1071. <https://doi.org/10.1111/j.14610248.2008.01219.x>.
- Cotrufo, M.F., Ranalli, M.G., Haddix, M.L., Six, J., Lugato, E., 2019. Soil carbon storage informed by particulate and mineral-associated organic matter. *Nat. Geosci.* 12, 989. <https://doi.org/10.1038/s41561-019-0484-6>.
- Crow, S.E., Lajtha, K., Filley, T.R., Swanston, C.W., Bowden, R.D., Caldwell, B.A., 2010. Sources of plant-derived carbon and stability of organic matter in soil: implications for global change. *Glob. Chang. Biol.* 15, 2003–2019. <https://doi.org/10.1111/j.13652486.2009.01850.x>.
- Cruz, A.F., Hamel, C., Hanson, K., Selles, F., Zentner, R.P., 2009. Thirty-seven years of soil nitrogen and phosphorus fertility management shapes the structure and function of the soil microbial community in a Brown chernozem. *Plant Soil* 315, 173–184. <https://doi.org/10.1007/s11104-008-9742-x>.
- Cusack, D.F., 2013. Soil nitrogen levels are linked to decomposition enzyme activities along an urban-remote tropical forest gradient. *Soil Biol. Biochem.* 57, 192–203. <https://doi.org/10.1016/j.soilbio.2012.07.012>.
- De Boer, W., Folman, L.B., Summerbell, R.C., Lynne, B., 2005. Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiol. Rev.* 29, 795–811. <https://doi.org/10.1016/j.femsre.2004.11.005>.
- Dungait, J.A.J., Hopkins, D.W., Gregory, A.S., Whitmore, A.P., 2012. Soil organic matter turnover is governed by accessibility not recalcitrance. *Glob. Chang. Biol.* 18, 1781–1796. <https://doi.org/10.1111/j.1365-2486.2012.02665.x>.
- Eberwein, J.R., Oikawa, P.Y., Allsman, L.A., Jenerette, G.D., 2015. Carbon availability regulates soil respiration response to nitrogen and temperature. *Soil Biol. Biochem.* 88, 158–164. <https://doi.org/10.1016/j.soilbio.2015.05.014>.
- Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* 10, 1135–1142. <https://doi.org/10.1111/j.1461-0248.2007.01113.x>.
- Fan, F., Yu, B., Wang, B., George, T.S., Yin, H., Xu, D., Li, D., Song, A., 2019a. Microbial mechanisms of the contrast residue decomposition and priming effect in soils with different organic and chemical fertilization histories. *Soil Biol. Biochem.* 135, 213–221. <https://doi.org/10.1016/j.soilbio.2019.05.001>.
- Fan, Y., Zhong, X., Lin, T.-C., Lyu, M., Wang, M., Hu, W., Yang, Z., Chen, G., Guo, J., Yang, Y., 2019b. Effects of nitrogen addition on DOM-induced soil priming effects in a subtropical plantation forest and a natural forest. *Biol. Fertil. Soils* 56, 205–216. <https://doi.org/10.1007/s00374-019-01416-0>.
- Fang, H., Mo, J., Peng, S., Li, Z., Wang, H., 2007. Cumulative effects of nitrogen additions on litter decomposition in three tropical forests in southern China. *Plant Soil* 297, 233–242. <https://doi.org/10.1007/s11104-007-9339-9>.
- Fang, X.M., Zhang, X.L., Chen, F.S., Zong, Y.Y., Bu, W.S., Wan, S.Z., Luo, Y., Wang, H., 2019. Phosphorus addition alters the response of soil organic carbon decomposition to nitrogen deposition in a subtropical forest. *Soil Biol. Biochem.* 133, 119–128. <https://doi.org/10.1016/j.soilbio.2019.03.005>.
- Fontaine, S., Henault, C., Aamor, A., Bdioui, N., Bloor, J.M.G., Maire, V., Mary, B., Revaillet, S., Maron, P.A., 2011. Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. *Soil Biol. Biochem.* 43, 86–96. <https://doi.org/10.1016/j.soilbio.2010.09.017>.
- Freeman, C., Ostle, N.J., Fenner, N., Kang, H., 2004. A regulatory role for phenol oxidase during decomposition in peatlands. *Soil Biol. Biochem.* 36, 1663–1667. <https://doi.org/10.1016/j.soilbio.2004.07.012>.
- Frostegard, A., Baath, E., 1996. The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. *Biol. Fertil. Soils* 22, 59–65. <https://doi.org/10.1007/bf00384433>.
- Garcia-Palacios, P., Shaw, E.A., Wall, D.H., Haettenschwiler, S., 2016. Temporal dynamics of biotic and abiotic drivers of litter decomposition. *Ecol. Lett.* 19, 554–563. <https://doi.org/10.1111/ele.12590>.
- Ghafoor, A., Poeplau, C., Katterer, T., 2017. Fate of straw- and root-derived carbon in a Swedish agricultural soil. *Biol. Fertil. Soils* 53, 257–267. <https://doi.org/10.1007/s00374-016-1168-7>.
- Grace, J., Malhi, Y., Meir, P., Higuchi, N., 2001. Productivity of tropical rain forests. *Tropical Global Productivity*. Academic Press, San Diego, pp. 401–426.
- Guo, L.B., Gifford, R.M., 2010. Soil carbon stocks and land use change: a meta analysis. *Glob. Chang. Biol.* 8, 345–360. <https://doi.org/10.1046/j.1354-1013.2002.00486.x>.
- Hagedorn, F., Spinnler, D., Siegwolf, R., 2003. Increased N deposition retards mineralization of old soil organic matter. *Soil Biol. Biochem.* 35, 1683–1692. <https://doi.org/10.1016/j.soilbio.2003.08.015>.
- Harrell, F., 2021. *Hmisc: Harrell Miscellaneous*. R Package Version 4.5-0.
- Hobbie, S.E., Vitousek, P.M., 2000. Nutrient limitation of decomposition in Hawaiian forests. *Ecology* 81, 1867–1877. [https://doi.org/10.1890/0012-9658\(2000\)081\[1867:Nlodih\]2.0.Co;2](https://doi.org/10.1890/0012-9658(2000)081[1867:Nlodih]2.0.Co;2).
- Hou, E., Luo, Y., Kuang, Y., Chen, C., Lu, X., Jiang, L., Luo, X., Wen, D., 2020. Global meta-analysis shows pervasive phosphorus limitation of aboveground plant production in natural terrestrial ecosystems. *Nat. Commun.* 11, 637. <https://doi.org/10.1038/s41467-020-14492-w>.
- Hui, D., Porter, W., Phillips, J.R., Aidar, M.P.M., Lebreux, S.J., Schadt, C.W., Mayes, M.A., 2020. Phosphorus rather than nitrogen enhances CO₂ emissions in tropical forest soils: evidence from a laboratory incubation study. *Eur. J. Soil Sci.* 71, 495–510. <https://doi.org/10.1111/ejss.12885>.
- Jacobson, T.K.B., Bustamante, M.M.C., 2014. Leaf litter decomposition and nutrient release under nitrogen, phosphorus and nitrogen plus phosphorus additions in a savanna in central Brazil. *Nitrogen Deposition, Critical Loads and Biodiversity*. Springer, Dordrecht, pp. 155–163.
- Janssens, I.A., Dieleman, W., Luysaert, S., Subke, J.A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A.J., Grace, J., Matteucci, G., Papale, D., Piao, S.L., Schulze, E.D., Tang, J., Law, B.E., 2010. Reduction of forest soil respiration in response to nitrogen deposition. *Nat. Geosci.* 3, 315–322. <https://doi.org/10.1038/ngeo844>.
- Jing, X., Yang, X., Ren, F., Zhou, H., Zhu, B., He, J.S., 2016. Neutral effect of nitrogen addition and negative effect of phosphorus addition on topsoil extracellular enzymatic activities in an alpine grassland ecosystem. *Appl. Soil Ecol.* 107, 205–213. <https://doi.org/10.1016/j.apsoil.2016.06.004>.
- Jing, Z., Chen, R., Wei, S., Feng, Y., Zhang, J., Lin, X., 2017. Response and feedback of C mineralization to P availability driven by soil microorganisms. *Soil Biol. Biochem.* 105, 111–120. <https://doi.org/10.1016/j.soilbio.2016.11.014>.
- Knorr, M., Frey, S.D., Curtis, P.S., 2005. Nitrogen additions and litter decomposition: a meta-analysis. *Ecology* 86, 3252–3257. <https://doi.org/10.1890/05-0150>.
- Koegel-Knabner, L., Guggenberger, G., Kleber, M., Kandeler, E., Kalbitz, K., Scheu, S., Eusterhues, K., Leinweber, P., 2008. Organo-mineral associations in temperate soils: integrating biology, mineralogy, and organic matter chemistry. *J. Plant Nutr. Soil Sci.* 171, 61–82. <https://doi.org/10.1002/jpln.200700048>.
- Kuramae, E.E., Hillekens Remy, H.E., Hollander Mattias, D., van der Heijden Marcel, G.A., van den Berg, M., van Straalen Nico, M., Kowalchuk, G.A., 2013. Structural and functional variation in soil fungal communities associated with litter bags containing maize leaves. *FEMS Microbiol. Ecol.* 84, 519–531. <https://doi.org/10.1111/1574-6941.12080>.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Kuzyakov, Y., 2010. Review: factors affecting rhizosphere priming effects. *J. Plant Nutr. Soil Sci.* 165, 66–70. [https://doi.org/10.1002/1522-2624\(200208\)165:4<382::AID-JPLN382>3.0.CO;2-%23](https://doi.org/10.1002/1522-2624(200208)165:4<382::AID-JPLN382>3.0.CO;2-%23).
- Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. *Soil Biol. Biochem.* 32, 1485–1498. [https://doi.org/10.1016/s0038-0717\(00\)00084-5](https://doi.org/10.1016/s0038-0717(00)00084-5).
- Lavallee, J.M., Soong, J.L., Cotrufo, M.F., 2020. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. *Glob. Chang. Biol.* 26, 261–273. <https://doi.org/10.1111/gcb.14859>.
- Lenth, R.V., 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means R package version 1.5.4.
- Li, J., Li, Z., Wang, F., Zou, B., Chen, Y., Zhao, J., Mo, Q., Li, Y., Li, X., Xia, H., 2014. Effects of nitrogen and phosphorus addition on soil microbial community in a secondary tropical forest of China. *Biol. Fertil. Soils* 51, 207–215. <https://doi.org/10.1007/s00374-014-0964-1>.
- Liu, L., Greaver, T.L., 2010. A global perspective on belowground carbon dynamics under nitrogen enrichment. *Ecol. Lett.* 13, 819–828. <https://doi.org/10.1111/j.1461-0248.2010.01482.x>.
- Liu, L., Gundersen, P., Zhang, T., Mo, J., 2012. Effects of phosphorus addition on soil microbial biomass and community composition in three forest types in tropical China. *Soil Biol. Biochem.* 44, 31–38. <https://doi.org/10.1016/j.soilbio.2011.08.017>.
- Lu, X., Mo, J., Gilliam, F.S., Zhou, G., Fang, Y., 2010. Effects of experimental nitrogen additions on plant diversity in an old-growth tropical forest. *Glob. Chang. Biol.* 16, 2688–2700. <https://doi.org/10.1111/j.1365-2486.2010.02174.x>.
- Lu, X., Vitousek, P.M., Mao, Q., Gilliam, F.S., Luo, Y., Turner, B.L., Zhou, G., Mo, J., 2021. Nitrogen deposition accelerates soil carbon sequestration in tropical forests. *Proc. Natl. Acad. Sci. U. S. A.* 118, e2020790118. <https://doi.org/10.1073/pnas.2020790118>.
- Mackenzie, F.T., Vera, L.M., Lerman, A., 2002. Century-scale nitrogen and phosphorus controls of the carbon cycle. *Chem. Geol.* 190, 13–32. [https://doi.org/10.1016/s0009-2541\(02\)00108-0](https://doi.org/10.1016/s0009-2541(02)00108-0).
- Magill, A.H., Aber, J.D., 1998. Long-term effects of experimental nitrogen additions on foliar litter decay and humus formation in forest ecosystems. *Plant Soil* 203, 301–311. <https://doi.org/10.1023/a:1004367000041>.
- Manning, P., Saunders, M., Bardgett, R.D., Bonkowski, M., Bradford, M.A., Ellis, R.J., Kandeler, E., Marhan, S., Tschirko, D., 2008. Direct and indirect effects of nitrogen deposition on litter decomposition. *Soil Biol. Biochem.* 40, 688–698. <https://doi.org/10.1016/j.soilbio.2007.08.023>.
- McGroddy, M.E., Silver, W.L., de Oliveira, R.C., 2004. The effect of phosphorus availability on decomposition dynamics in a seasonal lowland Amazonian forest. *Ecosystems* 7, 172–179. <https://doi.org/10.1007/s10021-003-0208-y>.

- Mehnaz, K.R., Corneo, P.E., Keitel, C., Dijkstra, F.A., 2019. Carbon and phosphorus addition effects on microbial carbon use efficiency, soil organic matter priming, gross nitrogen mineralization and nitrous oxide emission from soil. *Soil Biol. Biochem.* 134, 175–186. <https://doi.org/10.1016/j.soilbio.2019.04.003>.
- Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63, 621–626. <https://doi.org/10.2307/1936780>.
- Michael, S., Strickland, Ernest, Osburn, Christian, Lauber, Noah, Fierer, Mark, 2009. Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. *Funct. Ecol.* 23, 627–636. <https://doi.org/10.1111/j.1365-2435.2008.01515.x>.
- Mo, J., Brown, S., Xue, J., Fang, Y., Li, Z., 2006. Response of litter decomposition to simulated N deposition in disturbed, rehabilitated and mature forests in subtropical China. *Plant Soil* 282, 135–151. <https://doi.org/10.1007/s11104-005-5446-7>.
- Mo, J., Zhang, W., Zhu, W., Gundersen, P., Fang, Y., Li, D., Wang, H., 2008. Nitrogen addition reduces soil respiration in a mature tropical forest in southern China. *Glob. Chang. Biol.* 14, 403–412. <https://doi.org/10.1111/j.1365-2486.2007.01503.x>.
- Mori, T., Shigehiro, I., Ryota, K., Agus, W., Joko, H., 2015. Phosphorus addition reduced microbial respiration during the decomposition of *Acacia mangium* litter in South Sumatra, Indonesia. *Tropics* 24, 113–118. <https://doi.org/10.3759/tropics.24.113>.
- Mori, T., Lu, X., Aoyagi, R., Mo, J., 2018. Reconsidering the phosphorus limitation of soil microbial activity in tropical forests. *Funct. Ecol.* 32, 1145–1154. <https://doi.org/10.1111/1365-2435.13043>.
- Nannipieri, P., Trasar-Cepeda, C., Dick, R.P., 2018. Soil enzyme activity: a brief history and biochemistry as a basis for appropriate interpretations and meta-analysis. *Biol. Fertil. Soils* 54, 11–19. <https://doi.org/10.1007/s00374-017-1245-6>.
- Neff, J.C., Townsend, A.R., Gleixner, G., Lehman, S.J., Turnbull, J., Bowman, W.D., 2002. Variable effects of nitrogen additions on the stability and turnover of soil carbon. *Nature* 419, 915–917. <https://doi.org/10.1038/nature01136>.
- Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Vasquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S., Grace, J., 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282, 439–442. <https://doi.org/10.1126/science.282.5388.439>.
- Poelau, C., Bolinder, M.A., Kirchmann, H., Katterer, T., 2016. Phosphorus fertilisation under nitrogen limitation can deplete soil carbon stocks: evidence from Swedish meta-replicated long-term field experiments. *Biogeosciences* 13, 1119–1127. <https://doi.org/10.5194/bg-13-1119-2016>.
- Poelau, C., Katterer, T., Leblans, N.I.W., Sigurdsson, B.D., 2017. Sensitivity of soil carbon fractions and their specific stabilization mechanisms to extreme soil warming in a subarctic grassland. *Glob. Chang. Biol.* 23, 1316–1327. <https://doi.org/10.1111/gcb.13491>.
- Qiu, Q., Wu, L., Ouyang, Z., Li, B., Xu, Y., 2016. Different effects of plant-derived dissolved organic matter (DOM) and urea on the priming of soil organic carbon. *Environ SciProcess Impacts* 18, 330–341. <https://doi.org/10.1039/c5em00446b>.
- R Core Team, 2021. *R: A Language and Environment for Statistical Computing*.
- Ramankutty, N., Foley, J.A., Norman, J., McSweeney, K., 2002. The global distribution of cultivable lands: current patterns and sensitivity to possible climate change. *Glob. Ecol. Biogeogr.* 11, 377–392. <https://doi.org/10.1046/j.1466-822x.2002.00294.x>.
- Romani, A.M., Fischer, H., Mille-Lindblom, C., Tranvik, L.J., 2006. Interactions of bacteria and fungi on decomposing litter: differential extracellular enzyme activities. *Ecology* 87, 2559–2569. [https://doi.org/10.1890/0012-9658\(2006\)87\[2559:lobafo\]2.0.co;2](https://doi.org/10.1890/0012-9658(2006)87[2559:lobafo]2.0.co;2).
- Rosseel, Y., 2012. lavaan: an R package for structural equation modeling. *J. Stat. Softw.* 48, 1–36.
- Rousk, J., Baath, E., 2007. Fungal and bacterial growth in soil with plant materials of different C/N ratios. *FEMS Microbiol. Ecol.* 62, 258–267. <https://doi.org/10.1111/j.1574-6941.2007.00398.x>.
- Rowley, M.C., Grand, S., Verrecchia, E.P., 2018. Calcium-mediated stabilisation of soil organic carbon. *Biogeochemistry* 137, 27–49. <https://doi.org/10.1007/s10533-017-0410-1>.
- Saiya-Cork, K.R., Sinsabaugh, R.L., Zak, D.R., 2002. The effects of long term nitrogen deposition on extracellular enzyme activity in an *Acer saccharum* forest soil. *Soil Biol. Biochem.* 34, 1309–1315. [https://doi.org/10.1016/S0038-0717\(02\)00074-3](https://doi.org/10.1016/S0038-0717(02)00074-3).
- Sayer, E.J., Heard, M.S., Grant, H.K., Marthews, T.R., Tanner, E.V.J., 2011. Soil carbon release enhanced by increased tropical forest litterfall. *Nat. Clim. Chang.* 1, 304–307. <https://doi.org/10.1038/nclimate1190>.
- Schermelleh-Engel, K., Moosbrugger, H., Müller, H., 2003. Evaluating the fit of structural equation models: tests of significance and descriptive goodness-of-fit measures. *Methods Psychol. Res. Online* 8, 23–74.
- Sinsabaugh, R.L., 2010. Phenol oxidase, peroxidase and organic matter dynamics of soil. *Soil Biol. Biochem.* 42, 391–404. <https://doi.org/10.1016/j.soilbio.2009.10.014>.
- Sterner, R.W., Elser, J.J., 2002. *Ecological Stoichiometry: The Biology of Elements From Molecules to the Biosphere*. Princeton University Press, Princeton, NJ, USA.
- Tabatabai, M.A., Bremner, J.M., 1969. Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. *Soil Biol. Biochem.* 1, 301–307. [https://doi.org/10.1016/00380717\(69\)90012-1](https://doi.org/10.1016/00380717(69)90012-1).
- Talbot, J.M., Bruns, T.D., Smith, D.P., Branco, S., Glassman, S.I., Erlandson, S., Vilgalys, R., Peay, K.G., 2013. Independent roles of ectomycorrhizal and saprotrophic communities in soil organic matter decomposition. *Soil Biol. Biochem.* 57, 282–291. <https://doi.org/10.1016/j.soilbio.2012.10.004>.
- Tian, J., Dungait, J.A.J., Lu, X.K., Yang, Y.F., Hartley, I.P., Zhang, W., Mo, J.M., Yu, G.R., Zhou, J.Z., Kuzyakov, Y., 2019. Long-term nitrogen addition modifies microbial composition and functions for slow carbon cycling and increased sequestration in tropical forest soil. *Glob. Chang. Biol.* 25, 3267–3281. <https://doi.org/10.1111/gcb.14750>.
- Tunlid, A., Hoitink, H.A.J., Low, C., White, D.C., 1989. Characterization of bacteria that suppress rhizoctonia damping-off in bark compost media by analysis of fatty-acid biomarkers. *Appl. Environ. Microbiol.* 55, 1368–1374. <https://doi.org/10.1128/AEM.55.6.1368-1374.1989>.
- Turner, B.L., Wright, S.J., 2014. The response of microbial biomass and hydrolytic enzymes to a decade of nitrogen, phosphorus, and potassium addition in a lowland tropical rain forest. *Biogeochemistry* 117, 115–130. <https://doi.org/10.1007/s10533-013-9848-y>.
- Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecol. Appl.* 20, 5–15. <https://doi.org/10.1890/08-0127.1>.
- Wang, F., Li, J., Wang, X., Zhang, W., Zou, B., Neher, D.A., Li, Z., 2014. Nitrogen and phosphorus addition impact soil N₂O emission in a secondary tropical forest of South China. *Sci. Rep.* 4, 05615. <https://doi.org/10.1038/srep05615>.
- Wang, C., Mori, T., Mao, Q., Zhou, K., Wang, Z., Zhang, Y., Mo, H., Lu, X., Mo, J., 2020. Long-term phosphorus addition downregulates microbial investments on enzyme productions in a mature tropical forest. *J. Soils Sediments* 20, 921–930. <https://doi.org/10.1007/s11368-019-02450-z>.
- Wang, F., Harindintwali, J.D., Yuan, Z., Wang, M., Wang, F., Li, S., Yin, Z., Huang, L., Fu, Y., Li, L., Chang, S.X., Zhang, L., Rinklebe, J., Yuan, Z., Zhu, Q., Xiang, L., Tsang, D.C.W., Xu, L., Jiang, X., Liu, J., Wei, N., Kästner, M., Zou, Y., Ok, Y.S., Shen, J., Peng, D., Zhang, W., Barceló, D., Zhou, Y., Bai, Z., Li, B., Zhang, B., Wei, K., Cao, H., Tan, Z., Zhao, L.-B., He, X., Zheng, J., Bolan, N., Liu, X., Huang, C., Dietmann, S., Luo, M., Sun, N., Gong, J., Gong, Y., Brahushi, F., Zhang, T., Xiao, C., Li, X., Chen, W., Jiao, N., Lehmann, J., Zhu, Y.-G., Jin, H., Schäffer, A., Tiedje, J.M., Chen, J.M., 2021. Technologies and perspectives for achieving carbon neutrality. *The Innovation* 2, 100180. <https://doi.org/10.1016/j.xinn.2021.100180>.
- Xiao, W., Chen, X., Jing, X., Zhu, B., 2018. A meta-analysis of soil extracellular enzyme activities in response to global change. *Soil Biol. Biochem.* 123, 21–32. <https://doi.org/10.1016/j.soilbio.2018.05.001>.
- Yao, Q., Li, Z., Song, Y., Wright, S.J., Guo, X., Tringe, S.G., Tfaily, M.M., Pasa-Tolic, L., Hazen, T.C., Turner, B.L., Mayes, M.A., Pan, C., 2018. Community proteogenomics reveals the systemic impact of phosphorus availability on microbial functions in tropical soil. *Nat. Ecol. Evol.* 2, 499–509. <https://doi.org/10.1038/s41559-017-0463-5>.
- Zhang, J., Li, J., Fan, Y., Mo, Q., Li, Y., Li, Y., Li, Z., Wang, F., 2020. Effect of nitrogen and phosphorus addition on litter decomposition and nutrients release in a tropical forest. *Plant Soil* 454, 139–153. <https://doi.org/10.1007/s11104-020-04643-9>.
- Zhang, J., Sayer, E.J., Zhou, J., Li, Y., Li, Y., Li, Z., Wang, F., 2021. Long-term fertilization modifies the mineralization of soil organic matter in response to added substrate. *Sci. Total Environ.* 798, 149341. <https://doi.org/10.1016/j.scitotenv.2021.149341>.
- Zhao, J., Wang, F., Li, J., Zou, B., Wang, X., Li, Z., Fu, S., 2014. Effects of experimental nitrogen and/or phosphorus additions on soil nematode communities in a secondary tropical forest. *Soil Biol. Biochem.* 75, 1–10. <https://doi.org/10.1016/j.soilbio.2014.03.019>.
- Zheng, M., Huang, J., Chen, H., Wang, H., Mo, J., 2015. Responses of soil acid phosphatase and beta-glucosidase to nitrogen and phosphorus addition in two subtropical forests in southern China. *Eur. J. Soil Biol.* 68, 77–84. <https://doi.org/10.1016/j.ejsobi.2015.03.010>.
- Zhou, S., Huang, C., Han, B., Xiao, Y., Tang, J., Xiang, Y., Luo, C., 2017. Simulated nitrogen deposition significantly suppresses the decomposition of forest litter in a natural evergreen broad-leaved forest in the rainy area of Western China. *Plant Soil* 420, 135–145. <https://doi.org/10.1007/s11104-017-3383-x>.
- Zhu, B., Gutknecht, J.L.M., Herman, D.J., Keck, D.C., Firestone, M.K., Cheng, W., 2014. Rhizosphere priming effects on soil carbon and nitrogen mineralization. *Soil Biol. Biochem.* 76, 183–192. <https://doi.org/10.1016/j.soilbio.2014.04.033>.