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RESEARCH ARTICLE

Litter quality controls tradeoffs in soil carbon decomposition and replenishment in a subtropical forest

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Abstract

1. Species-rich forests can produce litter of varying carbon (C) and nitrogen (N) composition (i.e. quality), which can affect decomposition and play a central role in long-term soil organic carbon (SOC) accumulation. However, how differences in litter quality affect SOC decomposition and formation remains unclear over the full litter decomposition trajectory.
2. We followed the in situ complete decomposition of added ^{13}C-labelled high- (low C:N) and low-quality (high C:N) leaf-litter and its effect on particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions over 2 years in a natural subtropical forest.
3. We found that during *early* stages of decomposition, low-quality litter inputs decreased SOC via a positive priming effect (i.e. new C inputs favoured decomposition of native SOC), but these SOC losses were offset by SOC gains observed via a negative priming effect during decomposition of high-quality litter. In contrast, this pattern reversed during *late* stages of decomposition—SOC losses via a positive priming effect induced by high-quality litter were offset by SOC gains via a negative priming effect induced by low-quality litter. Over the full decomposition of litter, both high- and low-quality litter stimulated microbial breakdown of SOC tied to POM, but also replenished more persistent SOC that associated with soil minerals (MAOM). Altogether, we observed that low-quality litter formed twice as much new SOC as high-quality litter (24% vs. 12% of added litter-C). We extend the notion of the priming effect from primarily a negative role promoting losses of native SOC, to a functional role that can replenish persistent SOC.
4. *Synthesis*. Our measurements raise the possibility that, in species-rich forests, high- and low-quality litter decomposition play opposite but dynamically complementary roles in renewing POM—both by inducing its decomposition and

formation—while exclusively favouring MAOM formation, which can help explain how differences in litter quality favour SOC accumulation and persistence. Global change factors that shift plant community composition may ultimately affect the fate of soil C, as changes in litter quality may force soil transitions from sinks to sources or sources to sinks of atmospheric CO_2.

KEYWORDS
^{13}C-labelled tree litter, complementary effect, isotope tracer field experiment, litter quality, priming effect, species-rich forests

1 | INTRODUCTION

Forests are key components of the global carbon (C) cycle storing 39% of the total terrestrial organic C both below- and above-ground (Lal, 2005; Pan et al., 2011). Of the total forest inventory, tropical and subtropical forests represent among the most productive and diverse ecosystems on Earth, implying they can influence atmospheric carbon dioxide (CO_2) concentrations and, therefore, climate (Cernusak et al., 2013; Hickler et al., 2008). Indeed, a growing number of studies suggest that species-rich forests favour soil organic C (SOC) formation and storage, because these forests integrate litter of varying C and nitrogen (N) composition (i.e. quality) with downstream impacts on litter decomposition and long-term SOC storage (Chen et al., 2020; Huys et al., 2022; Lange et al., 2015). However, it remains unclear how forests with varying litter quality influence SOC gains and losses, particularly the role of tree litter quality in sequestering soil C (Chen et al., 2020, 2023; Handa et al., 2014).

Forest SOC stocks vary in response to multiple ecological processes that alter the balance between photosynthetic C inputs and C outputs via microbial respiration of soil organic matter (SOM). Plant species diversity may alter this balance by adding litter across a wide range of C:N and lignin:N ratios, thereby altering the 'quality' of the litter inputs and the fate of C in both the litter and SOM (Melillo et al., 1982; Prescott, 2010). Litter quality can alter SOM stocks by 'priming' microbial processes that either replenish (i.e. negative priming) or decompose SOM (i.e. positive priming; Adamczyk et al., 2019; Kuzyakov et al., 2000; Liang et al., 2018; Lyu et al., 2019). In this sense, low-quality litter inputs (high C:N and lignin:N) may favour SOM decomposition because microbes may need to mine N locked in SOM to satisfy nutritional demands required to break down low-quality litter. In contrast, high-quality litter inputs may replenish SOM because the litter itself may have enough N to satisfy microbial nutritional demands required to break down high-quality litter (Cheng, 1999; Lyu et al., 2018; Vesterdal et al., 2008), limiting the need to mine N locked in SOM (Fontaine et al., 2011). Nevertheless, a recent field-based study in a broad-leaved subtropical forest dominated by high-quality litter, found that inputs of high-quality litter induced a greater priming effect than inputs of low-quality litter (Lyu et al., 2019). In contrast, in a coniferous forest dominated by low-quality litter, inputs of either high- or low-quality litter had no impact on the priming effect (Lyu et al., 2019; Wang et al., 2023). Therefore, the magnitude of the priming effect on SOM may depend on the C:N ratio of the soil and the composition of tree species and their litter quality.

Determining how litter inputs of varying quality affect the magnitude and direction of the priming effect (i.e. decomposition or replenishment of SOM) remains an open question requiring detailed monitoring of SOC pools and fluxes. For instance, plant litter inputs may affect SOC by favouring microbial decomposition of particulate organic matter (POM) or mineral-associated organic matter (MAOM), each with different effects on overall SOM formation. This is because POM is considered accessible to microbes and relatively unprotected by the soil mineral matrix with fast turnover rates (Witzgall et al., 2021). In contrast, MAOM is considered physically and chemically protected by interactions with soil minerals and can persist in soils for millennia (Cotrufo et al., 2015), although some components of MAOM may cycle in the order of decades to centuries or even more rapidly (Córdova et al., 2018). Thus, the effect of species-rich forests on SOM may depend on how litter quality affects SOC pools that vary in turnover times (i.e. POM and MAOM).

Most studies evaluating the effect of litter inputs on SOC pools have focused on either litter or SOM decomposition over relatively short timescales (Lyu et al., 2019; Witzgall et al., 2021). Furthermore, most of these studies have relied on laboratory experiments (Huys et al., 2022) and have not yet quantified how differences in litter quality and litter-derived C may replenish SOC in situ, limiting our ability to predict how litter inputs and decay rates affect SOM formation. Out of the few short-term studies that measured SOC replenishment, it is clear that: (i) a surprisingly large amount of litter-C is sequestered in mineral soils during early stages of decomposition (Rubino et al., 2010; Sokol & Bradford, 2019; Soong & Cotrufo, 2015), and that (ii) high-quality litter favours the formation of relatively persistent MAOM. This is likely because microbes metabolize litter C with a high C use efficiency (CUE; the ratio of C retained in biomass vs. C respired) after adding high-quality litter, whereas chemically complex low-quality litter favours SOM losses (Cotrufo et al., 2013; Hatton et al., 2015; Mitchell et al., 2020). In this sense, if low-quality litter inputs are expected to induce positive priming and loss of SOC, then high-quality litter inputs would be expected to induce negative priming, possibly offsetting the outcome.

Therefore, questions remain on whether the input of low- and high-quality litter from species-rich forests may *complement* each other to offset litter-derived SOC losses and gains.

In this study, we quantified the effect of litter quality on SOM priming and replenishment in natural subtropical forests in southern China and traced litter-C incorporation into both POM and MAOM pools using high- and low-quality ^{13}C-labelled litter in situ. We hypothesized that: (i) low-quality litter inputs would prime SOC decomposition (positive priming) because microbes would need to mine N locked in SOM to break down the low-quality litter, whereas adding high-quality litter would replenish SOM and lose relatively less SOC because microbial nutritional demands would be met by the added litter; (ii) high-quality litter inputs would favour production of more persistent SOC (MAOM) than low-quality litter because high-quality litter increases CUE producing more of the microbial products that build MAOM (Cotrufo et al., 2019; Fissore et al., 2008; Giardina et al., 2001); and (iii) persistent SOC formed from high- or low-quality litter (MAOM) would complement and replenish priming-induced SOC losses after adding either high- or low-quality litter.

2 | MATERIALS AND METHODS

2.1 | Site description

Our study site was located in the Wuyi Mountain National Park, Fujian Province, China (27°33′–27°54′ N, 117°27′–117°51′ E). The Park was established in 1979 and is the largest area of intact subtropical forest (56,527 ha) in southeast China. Common broad-leaved species include *Castanopsis eyrie* (Champ.) Tutch., *Schima superba* Gardn. et Champ. and *Castanopsis carlesii* (Hemsl.) Hay. Coniferous tree species include *Pinus taiwanensis* with scattered *Cunninghamia lanceolata* (Lamb.) Hook., which account for 85% of overstorey basal area. These forests have not been logged for centuries and are protected by the Wuyi Mountain National Park. The mean annual temperature is 15.8°C and the mean annual precipitation is 2661 mm, mostly occurring as rain, most rain falls during the monsoon summer (Figure S1). Soils are predominantly fine-textured silty clay loams, are derived from sandstone, and are classified as yellow red soil according to the Chinese Soil Classification System (this is equivalent to an Ultisol in the United States Department of Agriculture [USDA] Soil Taxonomy classification system; Lyu et al., 2019).

2.2 | ^{13}C-labelled leaf litter addition experiment

We studied the above-ground decomposition of ^{13}C-labelled high- and low-quality litter, the ensuing priming effect, and the incorporation of litter-derived C into SOM pools over 2 years in mixed broad-leaved and coniferous forests (Figure S2). The high-quality litter was derived from *C. carlesii* and the low-quality litter from *C. lanceolata* (Table 1). These two tree species are widely distributed in subtropical China (Lyu et al., 2018; SFA, 2009) and have both the highest and lowest litter C:N ratio in our study site. Given that the average C:N requirements for microbial biomass is roughly 30:1 (Brady & Weil, 2002), we considered litter C:N <30 as high quality and >30 as low quality. We labelled *C. carlesii* and *C. lanceolata* seedlings using previously described pulse labelling methods (Lyu et al., 2018). Briefly, seedlings were grown inside a sealed chamber (2 × 1.8 × 1.5 m) over roughly 6 months during the whole growing season containing a bottle of dissolved ^{13}C-sodium carbonate (99% ^{13}C; Cambridge Isotope Laboratories Inc.),

TABLE 1 Soil (0–5 cm) and ^{13}C-labelled high-quality (*Castanopsis carlesii*) and low-quality (*Cunninghamia lanceolata*) litter properties. Values are means ± standard deviations (n = 5). Different letters in the same row indicate significant difference at α = 0.05.

		Litter[a]	
	Soil	High-quality	Low-quality
Carbon (g kg^{-1})	82.06 ± 8.82b	463.65 ± 4.46a	459.56 ± 1.78a
Nitrogen (g kg^{-1})	3.72 ± 0.34c	17.82 ± 0.05a	9.75 ± 0.05b
Phosphorus (g kg^{-1})	0.33 ± 0.01c	0.68 ± 0.03a	0.49 ± 0.01b
C/N	22.01 ± 0.56c	26.02 ± 0.27b	47.15 ± 0.43a
C/P	249.05 ± 19.84b	686.23 ± 35.84b	922.07 ± 5.21a
N/P	11.31 ± 0.78c	26.37 ± 1.38a	19.56 ± 0.11b
δ^{13}C (‰)	−28.06 ± 0.05c	44.56 ± 4.12b	68.13 ± 4.95a
pH	4.21 ± 0.24		
Sand (%)	29.95 ± 4.44		
Silt (%)	60.32 ± 3.48		
Clay (%)	9.73 ± 1.31		
Lignin (%)		11.90 ± 0.73b	15.50 ± 1.26a
Cellulose (%)		17.18 ± 0.81a	18.03 ± 0.96a
Lignin/N		6.69 ± 0.40b	15.90 ± 1.26a

[a]Data from Lyu et al. (2019). Soil was sampled within 10 cm of the mesocosms at the beginning of incubation.

which was exposed to HCl twice per month to produce a pulse of $^{13}CO_2$. After the enrichment, only the leaves were still green when harvested, that is, not litter in the true sense, oven-dried (48 h at 55°C), cut with scissors into small pieces (2–4 mm) and thoroughly mixed. Final litter enrichment and other properties are listed in Table 1.

The experiment was established as a split-plot design consisting of five 20 × 20 m blocks with a >10 m buffer zone between them (Figure S2a). Within each block, we randomly established three 5 × 5 m plots, and within each plot, we established nine mesocosms to replicate in triplicate each of the following treatments: Control (no litter added), high-quality ^{13}C-labelled litter (addition of *C. carlesii* litter), and low-quality ^{13}C-labelled litter (addition of *C. lanceolata* litter; Figure S2b,c). Therefore, each block contained 27 mesocosms (3 plots × 3 treatments/plot × 3 treatment replicates) for a total of 135 mesocosms across our 5 blocks (27 mesocosms/block × 5 blocks). The mesocosms were made from 20 cm long × 20 cm diameter PVC tubing. The mesocosms were installed by first placing each PVC tube into an iron sleeve and striking the top of the iron sleeve with a hammer until it reached a depth of 18 cm—we left 2 cm of the PVC tube above the soil surface to facilitate gas sampling. Once the mesocosm was in place, we pulled out the iron tube leaving the mesocosm behind (Figure S3). To help keep soil moisture inside mesocosms representative of field conditions, we drilled eight holes (1 cm diameter) into the sidewalls of each mesocosm to facilitate water exchange. These holes and the bottom of the mesocosms were covered with mesh screens (0.15 × 0.15 mm) before they were installed to exclude roots but not microbes like mycorrhizal fungi (Figure S3).

At the end of December 2016—roughly 6 months after installing the mesocosms—8.8 g of dried (48 h at 55°C) leaf litter for the high- and low-quality treatments were uniformly added to the soil surface of the mesocosms after removing the native litter (Figure S2c). Because both the high- and low-quality litter had similar C content (~46%; Table 1), each mesocosm received C at a rate equivalent to the annual leaf-litter C input (129 g C m^{-2}; Lyu et al., 2019). After adding the litter, we covered the top of each mesocosm with mesh screens (1 mm) to prevent unlabelled litter from entering the mesocosms. The addition of litter did not affect soil temperature and moisture throughout the experimental period (Figure S4).

2.3 | Soil sampling and analyses

In August 2017 and January 2019 (i.e. 8 and 24 months after adding litter), we destructively sampled one control, high- and low-quality litter mesocosm from each of the three plots per block (3 treatments × 3 plots = 9 mesocosms per block; Figure S2a). For each mesocosm, we first collected any remaining surface litter and then divided the soil into two depths: 0–5 cm and 5–10 cm (we were unable to detect the ^{13}C label in 10–18 cm depth soils and these were no longer used). We then made one composite soil sample for each depth for the three litter-addition treatments. This was done by mixing the three mesocosms—representing each treatment—that were harvested from each of the three plots in each block (see Figure S2). Therefore, we produced five composite samples per litter-addition treatment, for a total of 15 composite samples at each depth (1 composite sample per block × 3 treatments × 5 blocks). All samples were sieved through a 2-mm mesh within 24 h. The soils were then divided into two samples: one sample was stored at 4°C until analysis of enzyme activity, dissolved organic C and N (DOC and DON), inorganic N (NH_4^+ and NO_3^-) and microbial biomass C and N (MBC and MBN) within 7 days, and the other sample was air-dried and stored in airtight plastic bags until analysis of SOM fractions, ^{13}C abundance and the concentration of C within 1 month for all five replicates.

To trace the incorporation of litter-derived C into SOM fractions, we physically separated the 0–5 and 5–10 cm soils into distinct fractions (Lyu et al., 2017; Strickland & Sollins, 1987). Studies indicate that soil C accrual and persistence in soils can be best described by dividing SOM into pools of POM and a MAOM (Castellano et al., 2015; Cotrufo et al., 2015, 2019). These two fractions can be analytically separated by size and/or density. In this study, we used density separation to fractionate the light fraction SOM (POM; density <1.7 g cm^{-3}) from the heavy fraction SOM (MAOM; density > 1.7 g cm^{-3}; Strickland & Sollins, 1987). Briefly, 10 g of the air-dried soil was sieved to remove litter and rocks larger than 2 mm and separate the litter fraction from the POM fraction. The sieved soil was then weighed into a 100-mL centrifuge tube and mixed with 50 mL NaI (density = 1.7 g cm^{-3}) to separate POM and MAOM fractions. Both POM and MAOM were washed with ~200 mL deionized water and dried for 24 h at 60°C, weighed, ground to a fine powder, and analysed for C and N content and for $^{13}C/^{12}C$ ratios. The mass recovery rate was 97 ± 1% and for C 103 ± 5% after the fractionation.

Soil and litter C and N concentrations were determined from the finely ground (<0.15 mm) subsamples of air-dried soil using a Vario MAX CN elemental analyser (Elementar Vario EL III). Before analysis of litter C and N, we took care to remove any soil adhering to the litter. Stable C isotope analyses were performed on a Finnigan MAT-253 Mass Spectrometer (Thermo Electron), coupled to an automatic, online elemental analyser (Flash EA 1112; Thermo Electron) using oven-dried (60°C to constant weight) soil and litter samples. The methods for analysing extracellular enzyme activity, DOC, DON, MBC, MBN and inorganic N are provided in the Supporting Information. Extracellular enzyme activity was only measured 8 months after establishing the litter treatments.

2.4 | Soil CO_2 flux and its carbon-isotopic signature

We measured monthly CO_2 fluxes from January 2017 to December 2018 using static chambers connected to a LI-8100 soil CO_2 flux system (LI-COR Inc.). We used a removable chamber (diameter = 20 cm, height = 22 cm) to collect gas samples from each mesocosm for $\delta^{13}C\text{-}CO_2$ analysis. To measure $\delta^{13}C\text{-}CO_2$, we used 50-mL plastic syringes to collect three 30-mL gas samples every 20 min for 1 h from the sealed mesocosm chambers, and then injected the samples into 50-mL pre-evacuated gas bags. Air temperature within each

experimental chamber was measured with a mercury thermometer at the time of sample collection.

Isotopic $\delta^{13}C$ analyses for CO_2 were conducted with an isotope ratio mass spectrometer (Finnigan MAT-253; Thermo Electron) at the Stable Isotope Mass Spectrometry Laboratory at Fujian Normal University within 7 days. The $\delta^{13}C$ values are expressed as per mil (‰) relative to the Pee Dee Belemnite standard. The accuracy, as determined by comparing the measured values to the known value of an internal laboratory standard (IAEA), was better than 0.12‰ for $\delta^{13}C$.

2.5 | Partitioning of C sources in CO_2, soil fractions and priming effect calculations

We used a mixing model to calculate $\delta^{13}C$-CO_2 (δ_E) values at a series of time points (Ohlsson et al., 2005):

$$\delta_E = \frac{\left(\delta_S C_0 - \delta_0 C_0 + \delta_S R_E t\right)}{R_E t}, \quad (1)$$

where δ_s is the $\delta^{13}C$ of the CO_2 at time t, δ_0 is the measured $\delta^{13}C$ at time $t=0$, C_0 the measured CO_2 concentration at time $t=0$ and R_E is the evolution rate of CO_2 determined from linear regression analyses of CO_2 concentrations in the samples (for details see Lyu et al., 2019). We used linear regression models over a 40-min period to estimate the CO_2 emission rate of change over time. Regression coefficients were greater than 0.9.

The litter-derived C contribution to the bulk soil, POM and MAOM pools was also determined with an isotope mixing model (Subke et al., 2004):

$$f_{litter} = \left(\delta_s - \delta_{control}\right) / \left(\delta_{litter} - \delta_{control}\right), \quad (2)$$

where f_{litter} is the fraction of the litter-derived C contributing to the POM and MAOM pools, δ_s and $\delta_{control}$ are the $\delta^{13}C$ values of the bulk soil, POM and MAOM from the litter addition plots (δ_s) and the Control plots ($\delta_{control}$). For bulk soil and SOM fractions, the $\delta_{control}$ average values across all Control plots were used. δ_{litter} is the $\delta^{13}C$ value of the initial litter. The amount of litter-derived C in these pools was obtained by multiplying the f_{litter} values by the corresponding mass of C in each pool.

We calculated the priming effect of adding litter as:

$$\text{Priming effect} = (Rs \text{ soil with litter}) - (Rs \text{ control}), \quad (3)$$

where '*Rs*' is the CO_2 emitted from control and litter-amended soils.

We calculated SOC formation efficiency as: SOC gained/litter-C lost × 100 (%).

2.6 | Statistical analyses

We used linear mixed models (LMMs) to analyse the temporal effects of adding different quality leaf-litter on total soil CO_2 flux, litter decomposition and the priming effect. In the models, block and plots (two levels) were treated as random effects, and treatments (mesocosms), sampling time and their interaction were modelled as fixed effects. A *t*-test was used to analyse the differences in litter-derived C incorporated into POM and MAOM pools between the high- and low-quality litter treatments. The LMM was also used to detect the effects of litter quality on DOC, DON, MBC, MBN, inorganic N, enzyme activities and soil-derived C in both POM and MAOM pools. In these models, blocks were treated as a random effect, and treatments (mesocosms), sampling time and their interaction were modelled as fixed effects. We used a quadratic model to simulate the maximum values for litter-derived CO_2 (y) and their corresponding time of production (x). Extreme value analysis was used to simulate the priming effect maximum and minimum values after adding high- and low-quality litter (Gilleland et al., 2013). All statistics were undertaken using R 4.0.0 (R Core Team, 2020) using the lme4 (Bates et al., 2015) R packages.

3 | RESULTS

3.1 | Soil respiration, litter decomposition and priming of native soil carbon

The total soil respiration (SOC + litter) rate was higher when we added litter in either the high- ($p=0.046$) or low-quality litter treatments ($p=0.032$) compared to Control treatments during the first 8 months of litter decomposition (January 2017–August 2017; Figure 1a). However, this trend reversed from 8 to 14 months after adding litter (September 2017–February 2018); the total respiration rate was higher in Control treatments than in either high- or low-quality litter treatments ($p<0.05$, Figure 1a). Fourteen months after adding litter (March 2018–September 2018), the total respiration rate was higher in high-quality litter treatments than in either low-quality litter or Control treatments ($p<0.05$), but no difference was observed between low-quality litter and Control treatments (Figure 1a).

The cumulative litter-derived CO_2 was significantly higher in high-quality litter treatments than in low-quality litter treatments ($p=0.022$, Figure 2a). Using a quadratic model in our in situ incubations, we show that the high-quality litter-derived cumulative CO_2 reached a maximum equivalent to 84% of the total litter-C (108 g $C\,m^{-2}$) at day 545, whereas the Low-quality litter treatments reached their maximum value (88 g $C\,m^{-2}$, equivalent to 68% of total litter-C) after 715 days (Figure 2a). During the early stages of litter decomposition (January–August 2017), the C:N of the high-quality litter increased (lowering its quality), whereas the C:N of the low-quality litter decreased (increasing its quality; Figure S5).

The low-quality litter inputs favoured decomposition of SOC (positive priming effect) over the first 8 months after adding litter (Figure 1b), but favoured replenishment thereafter (negative priming). In contrast, the high-quality litter favoured replenishment of SOC over the first 14 months after adding litter, but favoured

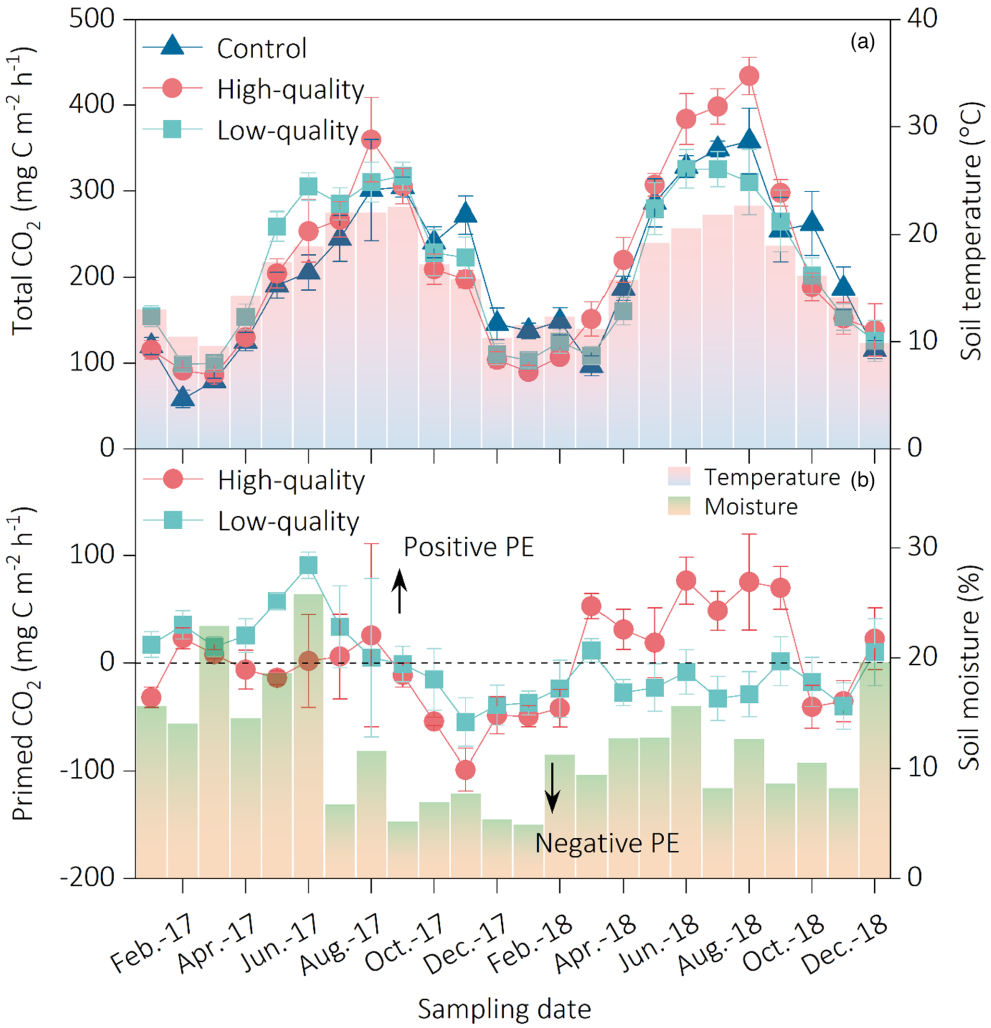

FIGURE 1 Effects of adding high- and low-quality litter on respiration and the priming effect (PE) in a mixed-species forest. Soil CO_2 emissions derived from: (a) soil organic matter (SOM) and added litter, (b) priming of SOM over 2 years after adding litter. Squares, circles and triangles with error bars represent means ± standard errors ($n = 5$). Bars represent soil temperature (a) and volumetric water content (b) on the secondary *y* axis.

decomposition of SOC thereafter (positive priming; Figures 1b and 2b). The amount of SOC decomposed via positive priming after adding low-quality litter was statistically equivalent to the SOC replenished via negative priming by high-quality litter during early stages of decomposition (January 2017–August 2017; Figure 2). In contrast, during late stages of litter decomposition (>14 months), this trend reversed; the amount of SOC decomposed via positive priming after adding high-quality litter was statistically equivalent to the SOC replenished via negative priming by low-quality litter (Figure 2b). Overall, we did not observe litter-induced SOC decomposition or replenishment once 95% of the litter C was lost, approximately 2 years after adding the litter (Figure 2b). Moreover, we found that the priming effect induced by high-quality litter was positively correlated with soil temperature ($r^2 = 0.14$, $p < 0.001$; Figure 3a), whereas the priming effect induced by low-quality litter was positively correlated with soil moisture ($r^2 = 0.29$, $p < 0.001$; Figure 3b).

3.2 | Carbon decomposition and formation in POM and MAOM fractions

Litter-derived C was measured down to 10 cm in the mineral soil (Figure 4A); we explored deeper depths but did not detect the isotope label. The fraction of high-quality litter-derived C incorporated into both POM and MAOM in the top 5 cm was significantly higher than the fraction of low-quality litter C going into these pools 8 months after adding the litter ($p = 0.033$; Figure 4A). However, 24 months after adding the low-quality litter, this trend reversed; the fraction of low-quality litter-derived C incorporated into both POM and MAOM in the top 5 cm was significantly higher than the C incorporated into these pools from high-quality litter. These findings were further supported by our LMM results, showing that adding low-quality litter negatively affected native POM after 8 months ($p < 0.01$), adding high-quality litter negatively affected POM only after 24 months ($p < 0.01$, Figure 4A), and both

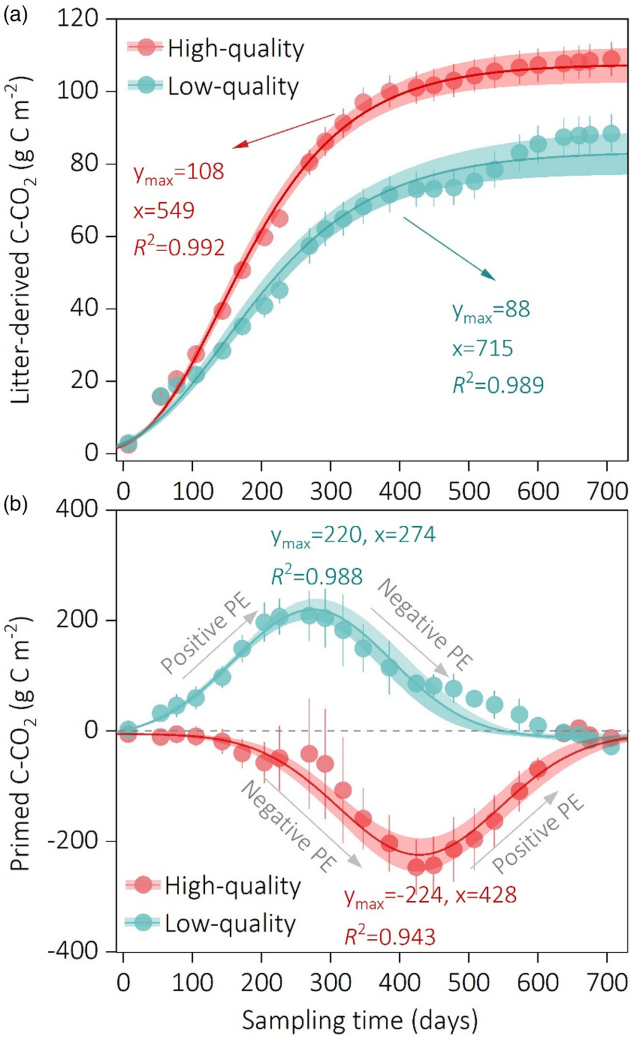

FIGURE 2 Cumulative litter-derived CO_2 and litter-induced priming effect (PE) over 2 years of litter decomposition in situ. (a) A quadratic model was used to estimate the maximum values for litter-derived CO_2 (y) as a function of days after adding litter (x). (b) An extreme value model was used to forecast the priming effect maximum and minimum values after adding high- and low-quality litter. Red and blue shaded areas represent the 95% confidence intervals.

litter types had no effects on MAOM after either 8 or 24 months ($p = 0.498$; Figure 4B).

The C storage of native POM in 0–5 cm soils decreased by 37% ($p = 0.011$) 24 months after adding high-quality litter and by 40% ($p = 0.007$) 24 months after adding low-quality litter (Figure 4B). In contrast to POM adding litter had no effect on native MAOM pools in 0–5 cm soils (Figure 4B). As observed with C, adding high- and low-quality litter significantly lowered the N content of POM with no effect on MAOM (Figure S6). In contrast to observations in 0–5 cm soils, adding either high- or low-quality litter had no effect on native POM or MAOM pools in the 5–10 cm soils.

Litter-derived C respiration was significantly higher in the high-quality litter treatments than in the low-quality litter treatments (Figure 5a). Consistent with this result, less litter-derived C remained in high-quality litter treatments, whereas more litter-derived C remained in low-quality litter treatments (Figure 5a); on average, 12% of the C in high-quality litter and 24% in low-quality litter was incorporated into SOM after 95% of the C in litter was lost with more litter-C transferred to MAOM than to POM ($p = 0.011$; Figure 5a). Over time, the low-quality litter-derived C incorporated into SOM increased from 9%, at 8 months, to 24%, at 24 months post-litter application. In contrast, the high-quality litter-derived C transferred to soil remained relatively stable ranging from 12.2%, after 8 months, to 11.8%, after 24 months post-litter application (Figure 5a). Overall, low-quality litter was more efficiently incorporated into SOM relative to high-quality litter (i.e. litter-derived C in SOM divided by C lost from the litter; Figure 5b), with high-quality litter increasing SOC by 12% and low-quality litter by 24% of the added litter C (Figure 6).

3.3 | Litter effects on soil microbial biomass and activity

Adding litter (both high- and low-quality) affected the activity of extracellular enzymes used for C acquisition; there was a positive effect on hydrolase activity (βG and CBH) relative to control plots (Figure S7a,b), but no effect on oxidase activity (PHO and PER; Figure S7c,d). With respect to nutrient-acquiring enzymes, adding low-quality litter significantly increased NAG by 100% and AP activity by 37% relative to control plots, but there was no effect after adding high-quality litter (Figure S7e,f).

Soil MBC ($p \leq 0.037$) and MBN ($p \leq 0.025$) increased 8 months after adding low-quality litter relative to control plots, whereas adding high-quality litter had no effect (Table S2). Adding low-quality litter increased microbial CUE while adding high-quality litter had no effect (Figure S8).

4 | DISCUSSION

Changes in litter quality often correlate with changes in the size of SOC stocks (Castellano et al., 2015), but whether and how differences in litter quality affect SOM decomposition and formation remains unclear, as studies have produced conflicting results and have mostly relied on laboratory experiments (Huys et al., 2022) and less so on in situ field observations tracking the fate of ^{13}C-labelled litter into SOM (Sayer et al., 2011). Here, we followed the in situ decomposition (>95% litter mass loss) of ^{13}C-labelled high- and low-quality litter from two tree species and determined its contribution to relatively labile (POM) and persistent (MAOM) SOM pools in a mixed subtropical forest. Consistent with our hypotheses, we found that during early stages of litter decomposition (first 8 months; January–August 2017) low-quality litter inputs triggered a positive priming effect, whereby microbes decomposed POM to acquire nutrients required to decompose the low-quality litter. In contrast to the low-quality litter, adding high-quality litter replenished SOC stocks by building relatively more persistent SOM that associated

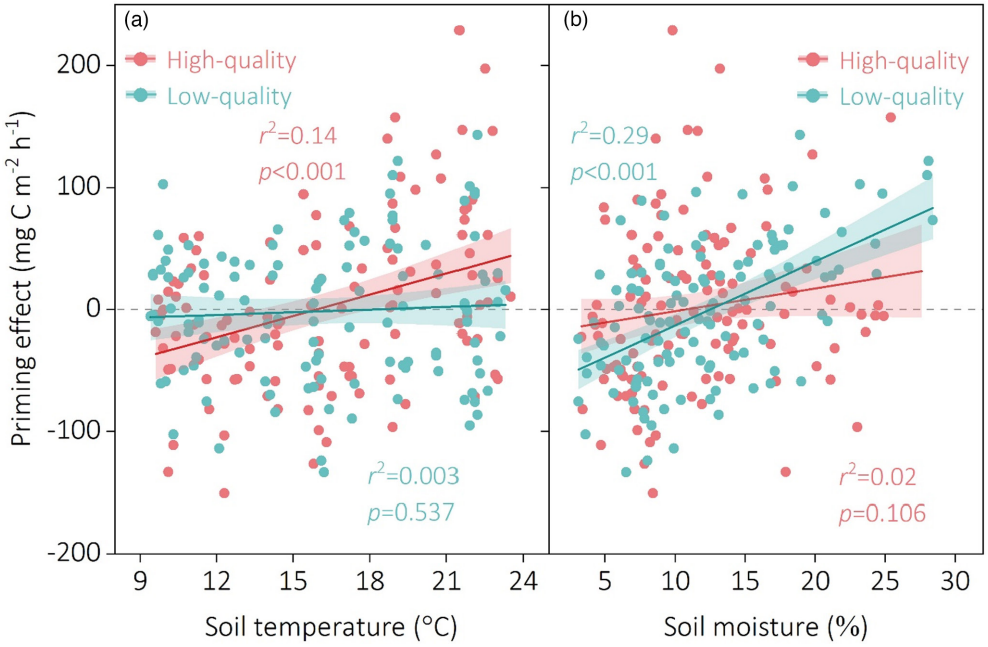

FIGURE 3 Relationships between the priming effect included by high- and low-quality litter with soil temperature (a) and moisture (b). Red and blue shaded areas represent the 95% confidence interval. *p*-values less than 0.05 represent significant relationships between the priming effect and soil temperature and moisture.

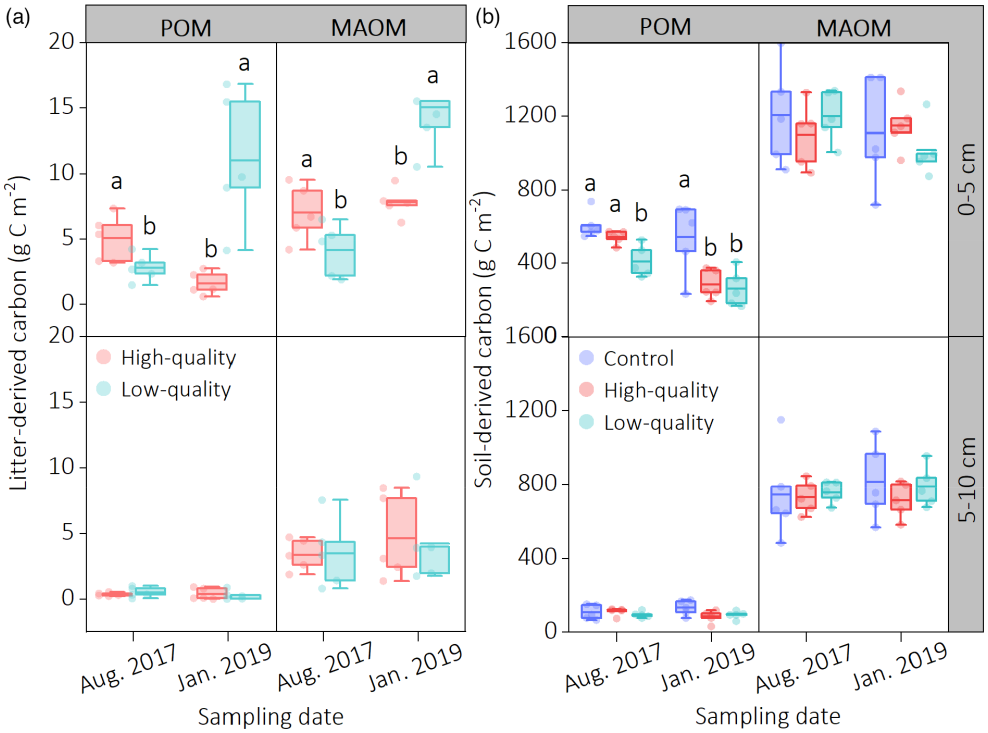

FIGURE 4 Allocations of (A) litter- and (B) soil-derived C (native C) to particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions. Measurements were made at both 0–5 and 5–10 cm soil depths approximately 8 months (August 2017) and 24 months (January 2019) after adding high- and low-quality litter. Different lowercase letters indicate significant differences between high- and low-quality litter treatments for each C fraction ($p < 0.05$).

with soil minerals (MAOM). Importantly, however, during the late stage of litter decomposition (>14 months), this trend reversed: the leftover high-quality litter induced SOM decomposition, whereas the leftover low-quality litter induced SOM replenishment. Our observations raise the possibility that a dynamic *complementarity effect* may alternate between SOM formation and decomposition as

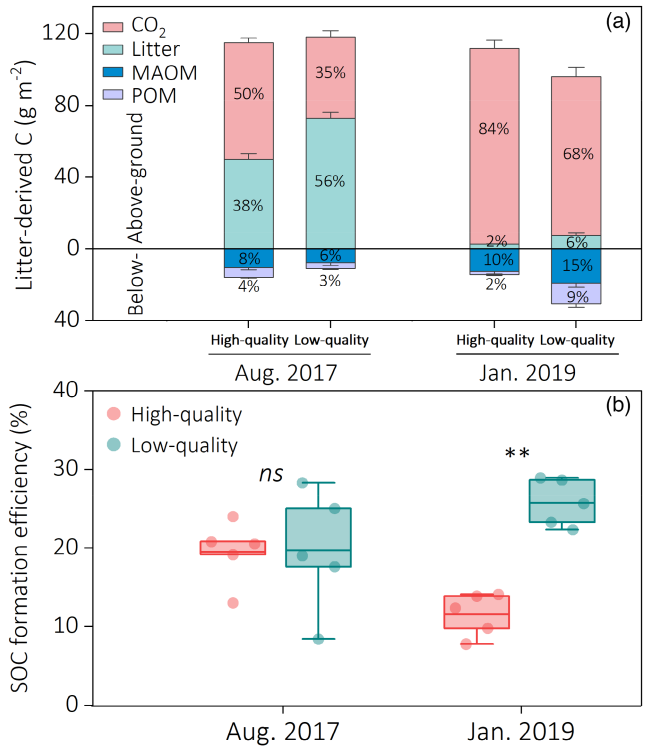

FIGURE 5 (a) The fate of litter-derived C in above- and below-ground C pools, and (b) the efficiency of soil organic carbon (SOC) formation relative to litter C lost (%) during 2 years after adding both high- and low-quality litter. The amount of litter C respired, remaining on the soil surface and recovered in particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions at 0–5 and 5–10 cm depths was quantified by isotopic mass balance. SOC formation efficiency was calculated as SOC gained ÷ litter C lost × 100. Values are means ± standard errors ($n = 5$). Stars represent significant differences between high- and low-quality litter treatments (**$p < 0.01$); ns, non-significant.

high- and low-quality litter decomposes in species-rich subtropical forests (Figure 6).

4.1 | Priming of POM, but not MAOM, during litter decomposition

During the early stage of litter decomposition, adding low-quality litter triggered a net positive priming effect (Figure 1a)—suggesting microbes mined SOM to acquire nutrients necessary to break down the low-quality litter. In support of this understanding, adding low-quality litter increased the activity of N-acquiring enzymes by 100% and the activity of P-acquiring enzymes by 37% relative to the control (Figure S7). In contrast to adding low-quality litter, adding high-quality litter did not trigger a positive priming effect and had no effect on either N- or P-acquiring enzymes, consistent with microbes not having to mine SOM to break down the high-quality litter in the early stage (Figure 4B; Vesterdal et al., 2008). However, during the late stages of litter decomposition (after 14 months), the quality of the high-quality litter declined (i.e. the C:N ratio in high-quality litter was greater than the low-quality litter; Figure S5) and decomposition patterns reversed; the high-quality litter stimulated SOM decomposition whereas the low-quality litter replenished SOM (Figure 2). Our findings suggest that litter nutrient status governs whether SOM is replenished or decomposed in these species-rich forests.

Many studies have shown adding low-quality litter can prime the decomposition of relatively old and persistent SOM (i.e. MAOM) if the N content in MAOM is higher than POM (Bingeman et al., 1953; Fontaine et al., 2007; Kuzyakov et al., 2000; Lü et al., 2015; Street et al., 2020). However, in sharp contrast to these observations, we found that adding low-quality litter was instead better at inducing decomposition of POM over MAOM (Figure 4) based on at least three observations: (i) neither adding high- nor low-quality litter altered the N in MAOM, whereas adding high- and low-quality litter decreased the N content of POM (Figure S6); (ii) the CO_2 released from positive priming was statistically equivalent to the amount of C lost from POM (220 ± 42 vs. 279 ± 45 g C m^{-2}; $p > 0.05$); and (iii) adding low-quality litter increased the activity of relatively labile C-degrading enzymes (βG and CBH) but not the activity of oxidative enzymes (PHO and PER) thought to be associated with breaking down more chemically complex/persistent C in MAOM (Li et al., 2018). These observations are consistent with the hypothesis that microbes mine N from SOM to degrade low-quality litter (Fontaine et al., 2011; Lyu et al., 2019), which is further supported by the significantly higher microbial biomass N present in low-quality litter plots relative to the Control (Table S2). Moreover, given that (i) MAOM is conceptualized as being less accessible to microbes relative to POM (Cotrufo et al., 2015; Sokol et al., 2018), (ii) that unlike laboratory studies that often sieve and homogenize soils, our soils were kept relatively undisturbed inside our in situ cores minimising microbial access to physically protected MAOM, and that (iii) N concentrations were fourfold greater in POM relative to MAOM per kg fraction (Figure S6a), it is not inconceivable POM was preferentially mined for N in this mixed species forest.

4.2 | Slow-decomposing litter formed more SOM than fast-decomposing litter

High-quality litter (fast-decomposing litter) is thought to promote MAOM formation with greater efficiency than low-quality litter (slow-decomposing litter; Córdova et al., 2018). Consistent with this understanding, we detected litter-derived C in soils down to 10 cm below the surface and found that high-quality litter replenished more SOM than low-quality litter during the early stage of litter decomposition; high-quality litter incorporated more C into MAOM (8%) relative to low-quality litter (6%; Figure 5a). However, over the long term, it was surprising to find that only 12% of the high-quality litter C associated with SOM after complete decomposition of the litter, whereas as greater amount of the low-quality litter C (24%) associated with SOM (Figure 5). Finding more C derived from low-quality litter in SOM was consistent with the higher microbial CUE measured after 8 months in low-quality litter plots relative to

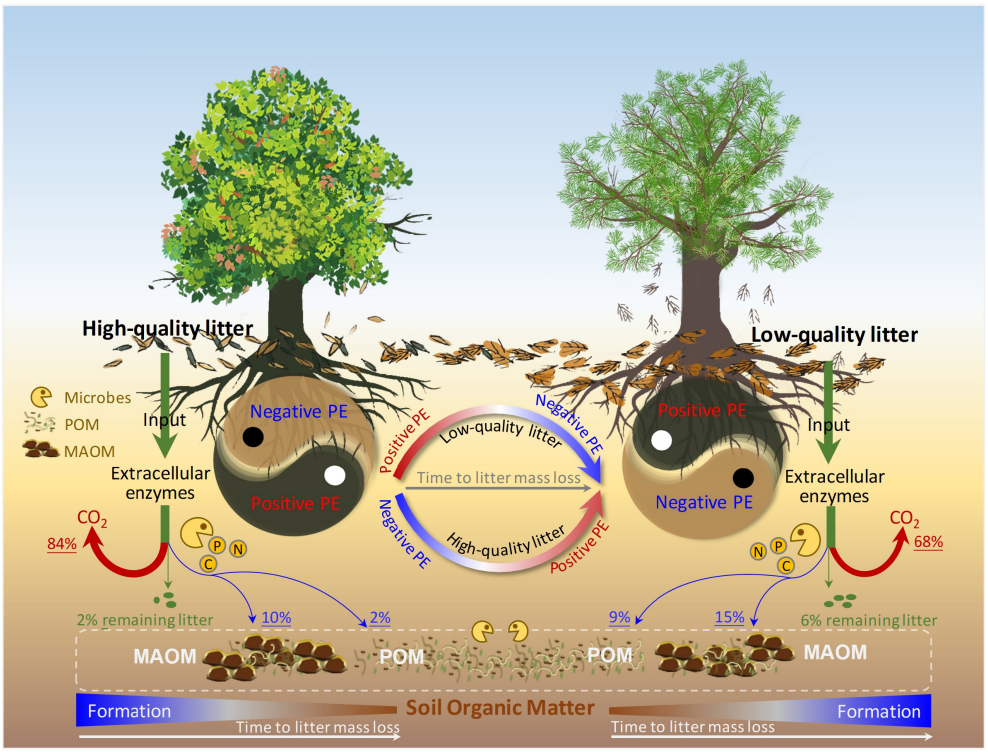

FIGURE 6 Conceptual framework for the loss and formation of soil organic matter (SOM) in species-rich forests. During *early* stages of litter decomposition, high-quality litter inputs replenish SOM via a negative priming effect (PE), whereas low-quality litter inputs decompose SOM via a positive PE. In contrast, during *late* stages of litter decomposition, the observed patterns reverse: high-quality litter inputs decompose SOM (positive PE) and low-quality litter inputs replenish SOM (negative PE). These apparent complementary dynamics that offset SOM replenishment and decomposition as high- and low-quality litter decompose are represented by the Ying and Yang under each type of litter quality and by the circle between them. The litter-induced positive PE depletes the relatively labile soil particulate organic matter (POM) pool, while forming more persistent mineral-associated organic matter (MAOM). Altogether, we observed that a positive PE induced by either high- or low-quality litter can be offset by a negative PE induced by litter of the opposite quality over the full length of litter decomposition. These observations raise the possibility that these tradeoffs in C gains and losses may be important for SOM formation as litter of different qualities mix in species-rich forests. Green arrows represent litter inputs, blue arrows represent negative PE or C replenishment and red arrows indicate positive PE or C decomposition. Arrow thickness represents the relative size of the C flux (% of added litter C). Percent values represent the contribution of litter-derived C (%).

high-quality litter plots (Figure S8). This finding may suggests that slow-decomposing litter incorporates more C to soil than fast-decomposing litter, which challenges results from previous studies. Our data suggest more complex dynamics control SOM formation than just the initial litter quality and, that studies evaluating these dynamics, require long-term in situ observations over the full decomposition of litter.

We acknowledge our experiment was not designed to determine the microscale mechanisms in charge of building SOM, and that while we conducted measurements in situ, we excluded the effect of roots on our measurements (e.g. potential priming induced by root exudates). However, our observations are consistent with the DOC microbial pathway proposed by Cotrufo et al. (2015), wherein DOC leached from litter is taken up by microbes to build SOM. In this sense, we found that adding both high- and low-quality litter increased soil DOC by 20% relative to the control during early stages of litter decomposition (Table S2), resembling an infrequent 'pulse' of C that was incorporated into SOM. In contrast, during the late stages of litter decomposition, DOC from low-quality litter resembled a consistent, low-volume 'drip' of C, ultimately forming more SOM over the long term. These conclusions are further supported by the fact that the accumulation of SOC per unit of litter-C mineralization was lower in soils amended with high-quality than low-quality litter (Figure 5b). While these interpretations are based on only 2 years of litter decomposition and the incorporation of litter-C into SOM pools, this was enough time to decompose 98% of the high-quality litter-C and 94% of the low-quality litter-C (Figure 5); maximum values for litter-derived CO_2 suggest the high-quality litter reached its peak after 549 days and the low-quality litter after 715 days (Figure 2a). Relative to previous studies, this rate of litter mass loss was high (Akira et al., 2020; Cotrufo et al., 2015; Lecerf et al., 2011), but may be the result of not enclosing litter in mesh bags—mesh bags may inhibit litter fragmentation and decelerate decomposition (Berg & McClaugherty, 2008; Cotrufo et al., 2019)—or to fast decomposition rates typical of subtropical climates (Handa et al., 2014). Taken together, inputs of high- and low-quality litter to soil may substantially influence SOC dynamics, helping to explain why it is difficult to reach a consensus regarding the effect of litter quality on SOM

decomposition and formation over the long term. Thus, it remains an open and pressing question to address whether high-quality litter should be characterized as a more efficient conduit to persistent SOC formation and, if so, what specific mechanisms underlie its transformation into SOM.

4.3 | Complementary mechanisms of SOC accumulation

Using our in situ experimental approach, our measurements revealed several unexpected effects of litter quality on SOM decomposition and replenishment. During the early stage of litter decomposition, low-quality litter inputs decreased SOC via positive priming, but these C losses were similar to gains observed in SOC after adding high-quality litter. However, during the late stage of litter decomposition, high-quality litter inputs primed SOM decomposition, producing SOC losses via positive priming that were similar to the gains in SOC from low-quality litter via negative priming (Figures 2 and 6). This unexpected reversal in priming effects over the full decomposition of litter may be a result of differential N mining in soil-derived SOM versus in the added litter, as the quality of both high- and low-quality litter changed as litter decomposed. That is, low- and high-quality litter inputs promoted both the microbial mining of SOM and its simultaneous replenishment since both litter types stimulated losses of POM, but gains in MAOM (Figure 6). This balance in SOC losses and gains was not only governed by differences in litter quality but also by environmental factors that affected decomposition. For example, increasing temperatures favoured SOM priming by high-quality litter, whereas decreasing soil moisture constrained SOM priming by low-quality litter (Figure 3). Taken together, whether SOC increases or decreases may vary as a function of high- and low-quality litter input rates and their response to a changing climate.

Our findings may raise the possibility of a 'complementarity' effect between litters of different quality (Figure 6), whereby interactions between high- and low-quality litter may affect SOM decomposition and formation, perhaps helping to explain why tree diversity increases soil C accrual (Chen et al., 2023). However, we acknowledge not being able to explicitly test for this interaction—the ^{13}C-labelled high- and low-quality litter values were not different enough to be mixed and added together, to then be able to separate their individual contributions in isotope space without substantially altering their properties (Whitman & Lehmann, 2015). Therefore, we opted for testing individual effects while recognizing it is possible the magnitude of a potential complementary effect may have been underestimated in our experiment. This is because low-quality litter may turn over faster when mixed with high-quality litter (Akira et al., 2020; Handa et al., 2014; Lecerf et al., 2011), further accelerating low-quality litter-derived C incorporation into SOM and possibly strengthening the complementary effect on SOC accumulation (Chen et al., 2023; Handa et al., 2014). Further experiments that consider the interaction of litter of different qualities across ecosystems will be required to confirm this mechanism and its potential effect on soil C storage.

In conclusion, the observed complementarity dynamics suggest that both high- and low-quality litter can stimulate microbial breakdown of SOC tied to POM, but also replenish more persistent SOC that associates with soil minerals (MAOM). This implies that the concept of priming, conventionally considered to play a negative role favouring the loss of SOC, may play a more functional role by also replenishing persistent SOC. Acknowledging these complementary dynamics can help improve forecasts of SOM formation and decomposition in systems where a mix of high- and low-quality litter dominates C inputs to the soil. Moreover, determining whether these complementary dynamics influence other forested ecosystems may help further understand how the balance between POM and MAOM formation/decomposition maintains active nutrient cycling and C storage. Given global changes that may alter the dominance and ecology of high- or low-quality litter tree species in species-rich forests, it is critical to recognize shifts in tree species composition may govern the fate of SOC as these systems may transition from sinks to sources of atmospheric CO_2.

AUTHOR CONTRIBUTIONS

Maokui Lyu, Peter M. Homyak, Guangshui Chen and Jinsheng Xie wrote the manuscript; Maokui Lyu and Jinsheng Xie designed and supervised the experiment; Maokui Lyu, Xiaoling Xiong, Minhuang Wang and Weisheng Lin carried out the measurements following the field incubation, collected and analysed data; Michael G. Ryan, Josep Peñuelas, Jordi Sardans and Yusheng Yang supervised the experiment and reviewed the manuscript. All authors discussed the data and contributed to the final draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available at the Dryad Digital Repository https://doi.org/10.5061/dryad.8931zcrwj (Lyu et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Monthly air temperature and precipitation during our 2-year litter decomposition experiment.

Figure S2. Schematic representation of our field experimental design.

Figure S3. Excavation and assembly of soil cores.

Figure S4. Monthly soil temperature and moisture across the whole experimental period.

Figure S5. Changes in C/N and N content of the remaining litter over our 2-year in-situ litter decomposition experiment.

Figure S6. Changes in (a, d) N content within the particulate organic matter (POM) and mineral-associated organic matter (MAOM) fraction, (b, e) the N content in relation to the total soil N pool for POM and MAOM, and (c, f) soil C/N ratios of the POM and MAOM fraction over 2-years after adding litter.

Figure S7. Potential activity of soil hydrolytic and oxidative enzymes involved in C-, N- and P-acquisition.

Figure S8. Microbial carbon use efficiency in response to litter inputs of different quality.

Table S1. Assayed soil extracellular enzymes, functions, and abbreviations used in this study.

Table S2. Changes in the contents ($mg\,kg^{-1}$) of soil carbon and nitrogen pools 8 and 24 months after adding litter.

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