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RESEARCH ARTICLE

Litter quality and site characteristics interact to affect the response of priming effect to temperature in subtropical forests

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Abstract

1. Forest litter inputs to soil can stimulate the decomposition of older soil organic matter (SOM) via a priming effect (PE). The magnitude and underlying mechanisms driving PE are poorly understood, with especially little know about how litter quality and site conditions affect PE in situ. Further, very few studies have examined PE in tropical and subtropical soils.
2. Here, we established low and high elevation sites (600 vs. 1,400 m a.s.l.) in the subtropical Wuyishan National Park, China, that differed with respect to mean annual temperature (MAT; ΔMAT = 4.2°C), vegetation, soil texture and soil moisture. We conducted a 1-year field incubation study at these two sites to compare PE induced by adding low- and high-quality ^{13}C-labelled leaf litter to soils.
3. At the low elevation site, additions of high-quality (low C/N) litter caused a PE that was 140% greater than the PE observed following additions of low-quality (high C/N) litter. In contrast, we saw no significant differences in PE between litter types at the high elevation site, perhaps because PE was not limited by substrate quality at this cooler, finer textured and higher soil moisture coniferous site. In addition, we found a negative relationship between home-field advantage (HFA) for litter decomposition and PE, indicating that specialized litter decomposer community driving HFA may not accelerate SOM decomposition via PE in the same way.
4. In line with our observed strong relationship between PE and the efficiency of priming (PE size per unit of mineralized litter C), PEs induced by the high- and low-quality litters were directed to microbial phosphorus (P) mining rather than nitrogen (N) mining. This interpretation aligns with observed increases in the activity of P acquiring extracellular enzymes, often described as phosphatases (P-tases), as well as the positive relationship between the PE, P-tase activity and the activity of C acquiring extracellular enzymes.

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5. Overall, this PE study across two contrasting sites highlights the important role of site characteristics and litter quality in regulating PE size. Further, we suggest that MAT may be a dominant driver of soil priming, through both the direct effects of litter quantity on labile substrate supply and the indirect effects of litter quality changes on downstream decomposer communities.

KEYWORDS
home-field advantage, litter quality, nutrient mining, priming effects, subtropical montane forests

1 | INTRODUCTION

By regulating atmospheric [CO_2], the decomposition of soil organic matter (SOM) is a critically important flux in the global carbon (C) cycle (IPCC, 2007), but the effects of environmental change on this flux are poorly constrained (Conant et al., 2011; Davidson & Janssens, 2006; Giardina & Ryan, 2000). One of these controls is hypothesized to be the quantity and quality of detrital inputs to soil, with both direct and indirect effects on SOM turnover and accrual. The effect of litter quantity and quality on SOM decomposition and formation are foundational drivers of SOM dynamics in models such as CENTURY (Parton, Ojima, Cole, & Schimel, 1994). Less studied is the hypothesized influence of fresh litter on the decomposition rates of SOM – commonly called the priming effect (PE; Bingeman, Varner, & Martin, 1953; Kuzyakov, Friedel, & Stahr, 2000). Tropical and subtropical forests represent among the most productive ecosystems on Earth, and so exert a disproportionately large influence on the global climate system (Cernusak et al., 2013; Hickler et al., 2008). Despite the importance of these systems, there are relatively few examinations of how litter inputs do or do not stimulate SOM decomposition or formation rates in these warm climate forests.

The priming of SOM decomposition rates by way of enhanced microbial activity has been found to be sensitive to both the quality and the quantity of plant-derived litter (Bader & Cheng, 2007; Kuzyakov et al., 2000; Talbot, Allison, & Treseder, 2008). It has been shown that the sustainability of priming can be several months even years after the complete degradation of the added organic matter (Fontaine et al., 2011; Sayer, Heard, Grant, Marthews, & Tanner, 2011, but see Giardina, Litton, Crow, & Asner, 2014). The direction of PE can also be highly variable, with some SOM decomposition rates responding to substrate additions increasing by up to 380% (Cheng, 1999; Lyu et al., 2018), while labile C additions in other studies suppressing by up to 50% rates of SOM decomposition (Kuzyakov, 2002; Kuzyakov et al., 2000; Lyu et al., 2018). Laboratory-based research on the mechanisms driving observed PE has been extensive, but results also have been contradictory (Chen et al., 2014; Fontaine, Mariott, & Abbadie, 2003; Kuzyakov et al., 2000). Because environmental change is likely to impact productivity, nutrient supply and so both litter quantity and quality, future studies of SOM priming would benefit from examining the effects of changing environmental conditions on PE as mediated by changing litter quality and quantity.

It is predicted that climate change will drive changes to SOC dynamics, but the mechanisms are complicated, and results to date mixed. Warming is known to increase forest productivity (Baldocchi et al., 2001) and alter species diversity (Cernusak et al., 2013; Hickler et al., 2008), including increased inputs of detrital C (Giardina et al., 2014) and changed litter quality (Cernusak et al., 2013) to soils. These direct effects of warming on both forest litter quantity and quality have led to the near universally held view that climate change can indirectly affect SOM dynamics through these litter effects. Finally, soil chemistry and physical properties influence below-ground processes including processing and stabilization of organic inputs to soil (Luo, Baldock, & Wang, 2017). Collectively, these various site characteristics (temperature, moisture, vegetation, soils) as drivers of PE are poorly explored, with few in situ studies examining PE, and especially limited representation from tropical and subtropical systems.

The effects of increasing litter quantity in cropland soils on the magnitude of PE have been shown to be positive until reaching a threshold, after which PE size does not increase (Guenet, Neill, Bardoux, & Abbadie, 2010). In contrast, there are large uncertainties regarding the effects of litter quality on PE, despite a clear theoretical mechanism for predicting PE size, such as microbial competition (Fontaine et al., 2003), microbial N mining (Fontaine et al., 2011) and microbially driven selective substrate decomposition (Cheng, 1999; Lyu et al., 2018). In some cases, theory has been challenged (e.g. N mining; Mason-Jones, Schmücker, & Kuzyakov, 2018), with microbial phosphorus (P) mining exerting controls over C cycling in low-P ecosystems (DeForest, 2019), such those found in the tropics and subtropics.

Micro-organisms generally favour high-quality (e.g. low C/N) over low-quality litter (e.g. high C/N) (Vesterdal, Schmidt, Callesen, Nilsson, & Gundersen, 2008), the later requiring elevated production of extracellular enzymes to metabolize (Fontaine et al., 2003). The addition of high-quality litter then is hypothesized to induce PE that is positive because such additions increase microbial activity, with additional supply of energy allowing microbes to metabolize otherwise inaccessible substrates. But it is also possible that high-quality litter additions negatively affect the decomposition of older SOM because micro-organisms preferential utilize the added fresh organic matter (Cheng, 1999; Lyu et al., 2018). The outcome of low-quality litter additions is more difficult to predict because the added substrates are on their own more difficult to utilize by microbes. Theoretically, we would anticipate that additions of low-quality substrates would lead

to smaller or even negative PE. However, experimental additions of low-quality substrates have elicited larger positive PE than additions of high-quality substrates, or even simple substrates such as root exudates (Fontaine et al., 2011; Kuzyakov, 2010).

How site characteristics of climate (temperature and moisture), vegetation type and soils (physical and chemical properties) interact to affect PE, and so SOM decomposition rates have been studied in a very limited way (Delgado-Baquerizo, Grinyer, Reich, & Singh, 2016), but can strongly influence PE. For example, microbial communities are dynamic and can adjust in response to changing litter quality such that the microbial players also can determine the magnitude and direction of a PE based on how quality of the dominant litter inputs has shaped the composition and structure of the microbial community. Explanations include the decomposer communities being specialized in the utilization of litter derived from the plants with which they are associated (Ayres, Steltzer, Berg, & Wall, 2009). For example, in a recent laboratory incubation experiment, PE was shaped by microbial home-field advantage (HFA) – specifically rates of litter decomposition and PE differ between home combinations of plant and litter versus away combinations (Di Lonardo et al., 2018). Critically, the strength and even occurrence of a litter based HFA can be influenced by interactions among climate, vegetation type including plant traits, and soil properties (Veen, Sundqvist, & Wardle, 2015). If HFA can influence litter decomposition, then logically, HFA should also influence the magnitude and direction of PE, with the magnitude and even direction of this influence being regulated by site characteristics. To our knowledge, no study has examined how HFA influences PE.

In this study, we established a pair of forested research sites at low and high elevation in Wuyishan National Park, China. Because the high elevation site is dominated by coniferous vegetation producing low-quality litter whereas the low elevation site is dominated by evergreen broad-leaved vegetation producing high-quality litter, this design provided a valuable opportunity to examine (a) the consequences of litter quality manipulations for SOM decomposition under diverse field and site conditions and (b) the relative importance of HFA versus quality of litter additions as competing constraints on PE. Based on observations that low-quality litter inputs can lead to microbial N mining due to the relatively low availability of N in low-quality litter (Fontaine et al., 2011), if HFA effects are weak, then we would anticipate that additions of low-quality litter would induce greater PEs than high-quality litter both at the high and low elevation site (H1a). Alternatively (H1b), if HFA effects are strong and operating across our two sites, then we would anticipate that HFA would drive the direction and magnitude PE following additions of low-quality litter at high elevation site, whereas HFA would drive the direction and magnitude of PE following additions of high-quality litter at low elevation site. If HFA effects are strong, such that HFA overwhelms the effects of sites factors, for example temperature, on litter decomposition, we then hypothesized that differences in litter decomposition rates between high and low elevation site would be greater for additions of low- versus high-quality litter (H2) because HFA at the cooler site would drive higher than predicted decomposition of low-quality litter, with the inverse being true for low-quality litter at the low elevation site. Conversely, HFA would accentuate an apparent temperature effect on the decomposition of high-quality litter because HFA would result in higher than expected litter decomposition rates at low elevation, with the inverse being true for high-quality litter at high elevation. In line with this hypothesis about HFA, litter quality and litter decomposition, and based on the concept of preferential substrate utilization (Cheng, 1999; Lyu et al., 2018), we hypothesized that the PE induced by high-quality litter would be smaller at the low versus high elevation site (H3) because additions of high-quality litter at low elevation would reduce utilization of low-quality SOM, whereas at high elevation, additions of high-quality litter would be used by the microbial community to mine SOM – giving the overall appearance of weak temperature sensitivity of PE. In contrast, additions of low-quality litter would not shift utilization to the added litter, with the microbial community rather using the lower quality litter to mine SOM for nutrients. At the high elevation site, a microbial community tuned to low-quality litter would preferentially utilize this substrate, which could shift utilization away from SOM, giving the overall appearance of a strong effect of temperature on PE.

2 | MATERIALS AND METHODS

2.1 | Site description and experimental design

We studied PE induced by applying different quality litters in two contrasting sites that differed with respect to vegetation, soils and climate via selecting two study sites, one at 600 m a.s.l. and another at 1,400 m a.s.l. (Figure S1) in the Wuyishan 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 natural forest (56,527 ha) in southeast China. These sites are located approximately 5.2 km from each other on Mashu Mountain. The low elevation site is typical of low elevation forests (200 ~ 800 m a.s.l.) in this region. The high elevation site is dominated by coniferous forest, which is typical of high elevations forests (1,000 ~ 1,800 m a.s.l.) in this region. The low elevation broad-leaved forests are dominated by *Castanopsis carlesii* and *Castanopsis eyrie*, which account for 78% of overstory basal area, while high elevation coniferous forests are dominated by *Pinus tanwanensis* and *Cunninghamia lanceolata*, which account for 85% of overstory basal area (Figure S1a; Bu et al., 2012; Huang et al., 2018). These forests appear to have been stable for centuries, were protected from disturbance after establishment of the national park and are the result of natural processes of mortality and regeneration.

The area has a subtropical monsoonal climate with mean annual temperatures of 18.2 and 14.0°C at low elevation (600 m a.s.l.) and high elevation (1,400 m a.s.l.), respectively. The annual rainfall (throughfall) of the low and high elevation site was 2,374 and 2,560 mm during our measurement year, respectively. However, the lower rainfall, higher temperature and coarser texture of the broadleaf site lead to lower mean annual soil water content compared with the cooler coniferous site (20.8 ± 1.8% vs. 31.7 ± 5.1%, respectively).

Soils at both sites are derived from sandstone parent material and are classified as yellow-red soil according to the Chinese Soil

Classification System, equivalent to an Ultisol in the United States Department of Agriculture (USDA) Soil Taxonomy classification system (Huang et al., 2018). Soil total C, N and P content, soil C/N at the high elevation site are significantly higher than at the low elevation site; soil pH is similar, but soil texture is finer at the high elevation site, perhaps explaining some of the nutrient differences. Bulk density is greater at the low elevation site, perhaps because of the lower organic matter and coarser texture of the soil (Table 1).

2.2 | Labelled ^{13}C-leaf litters

In our manipulative experiment, we used two litter types with contrasting qualities and physical structure. The high-quality litter was collected from *Castanopsis carlesii,* while low-quality litter was collected from *Cunninghamia lanceolate* (Table 2). These two species are widely distributed in subtropical China (Lyu et al., 2018; SFA, 2009), with *C. carlseii* occurring in the low elevation sites, and making up 60% of stand basal area for our plots. We also chose *C. lanceolata* because it is the dominant plantation tree that is planted in the region, accounting for 32% of all commercial plantations in southern China in terms of acreage or timber production (Piao et al., 2009; SFA, 2009).

We labelled *C. carlesii* and *C. lanceolata* seedlings using previously described pulse labelling methods (Lyu et al., 2018). Briefly, all seedlings of both species were moved into a transparent chamber for $^{13}CO_2$ pulse labelling twice monthly for six months. After 12 exposures to the label, we harvested the seedlings and clipped all the leaves with scissors. The final $\delta^{13}C$ of foliar material collected from the *C. carlesii* and *C. lanceolata* seedlings averaged 45‰ (CV = 9.2%) and 110‰ (CV = 6.1%), respectively. A low coefficient variation of the leaf $\delta^{13}C$ indicates that labelling was effective in creating homogeneous tissue $\delta^{13}C$.

TABLE 1 Properties of topsoil (0–5 cm) at the high elevation (1,400 m) and the low elevation (600 m). Values are *M* ± SD (*n* = 5)

	High elevation	Low elevation	*p*-value
Total carbon (g/kg)	60.2 ± 6.0	30.3 ± 5.1	**.036**
Total nitrogen (g/kg)	3.4 ± 0.87	2.0 ± 0.36	**.026**
Soil C/N	17.7 ± 0.98	15.2 ± 0.54	**.043**
Total phosphorus (g/kg)	0.62 ± 0.05	0.24 ± 0.02	**<.001**
pH	4.6 ± 0.11	4.8 ± 0.04	.089
Bulk density (g/cm^3)	0.56 ± 0.07	0.81 ± 0.15	**.023**
Sand (%)	27.1 ± 2.6	34.1 ± 3.9	**.023**
Silt (%)	56.8 ± 1.5	53.1 ± 3.4	.096
Clay (%)	16.2 ± 1.4	12.8 ± 0.5	**.014**

Note: Bold values indicate significant difference at *p*-value < .05.

TABLE 2 Properties of the two ^{13}C-enriched leaf litter types used in this study, high-quality (*Castanopsis carlesii*) and low-quality (*Cunninghamia lanceolata*)

	High-quality	Low-quality	*p*-value
Total carbon (%)	46.4 ± 0.45	46.0 ± 0.18	.055
Total nitrogen (%)	1.78 ± 0.01	0.97 ± 0.01	**<.001**
C/N	26.0 ± 0.27	47.2 ± 0.43	**<.001**
$\delta^{13}C$ (‰)	44.6 ± 4.12	110.0 ± 6.67	**<.001**
Cellulose (%)	17.2 ± 0.81	18.0 ± 0.96	.912
Lignin (%)	11.9 ± 0.73	15.5 ± 1.26	**.008**
Lignin/N	6.7 ± 0.40	15.9 ± 1.26	**.007**

Note: Values are *M* ± *SD*. The *p*-value indicates the result of a *t* test between the two litter types. Bold values indicate significant difference at *p*-value < .05.

2.3 | Field set-up

Field mesocosms for quantifying the high-quality and low-quality litter decomposition and soil C priming were constructed from PVC (Figure S1d). These chambers (diameter = 20 cm, height = 20 cm) were made by using 20 cm long, 20 cm diameter PVC tube stopper. To collect soil cores for the mesocosms, we placed each cylinder into an iron tube, striking on the top of iron tube until it reached a depth of 20 cm, after which we extracted the whole tube (Figure S2).

We established five 20 × 20 m plots at each of the two sites; at each site, two plots were located at the top, one at the middle and two at the bottom of the slope (Figure S1b). Each of the five plots was separated by at least five metres, and for statistical purposes, we treated each of the five plots as independent replicates (*n* = 5). In each plot, relying on a split-subplot design, we placed identified three randomly located subplots with each subplot receiving one of three mesocosm treatments: control (no litter addition); high-quality litter (addition of *C. carlesii* litter); and low-quality litter (addition of *C. lanceolate* litter), and repeated for each subplot in each of the five plots at two sites (Figure S1c and d). To ensure soil moisture was representative of the site, we drilled eight holes (diameter = 1 cm) in each mesocosm side wall to improve water exchange; to avoid soil loss, we covered the sides and bottom of the PVC chamber with nylon mesh (0.15 × 0.15 mm) before they were replaced into the soil (Figure S3). The nylon mesh also excluded root entry into the mesocosms. All the soil cores were inserted into soil to a depth of 18 cm, after which we applied the litter treatments. This an in situ litter incubation experiment ran for one year.

Leaf litter for high-quality and low-quality treatments was uniformly added to the surface of the mesocosms after removing the existing litter (Figure S1d). For each mesocosm receiving litter, we placed 8.8 g of one of the previously dried (48 hr at 55°C) litters onto the soil surface. The amount of litter was determined according to the average annual litterfall biomass of *C. carlesii* and *C. lanceolata* forests (~280 g/m^2) in subtropical region. Because the two leaf litters have similar C content (46%; Table 1), each mesocosm received C at a similar rate (129 g C/m^2). The top of each mesocosm was covered with a nylon mesh (1 mm) to prevent the input of

other litter. In total, 90 mesocosms were deployed at both sites (2 sites × 5 plots × 3 subplots × 3 treatments) (Figure S1). Mesocosms within a split-subplot were placed 15–30 cm away from each other to reduce heterogeneity among the mesocosms within each block.

2.4 | Soil sampling and analyses

In August of 2017, three mesocosms (control, high- and low-quality litter treatments) from each split-subplot were extracted, and then their topsoil (0–5 cm) collected after removing any remaining surface litter. All samples were immediately sieved through a 2-mm mesh (<24 hr). The soils were divided into two parts: one part was stored at 4°C until analyses within 7 days, and another part was air-dried and stored in airtight plastic bags until analysis within one month.

Total soil C and N contents 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, Germany). Soil texture was measured using a Mastersizer 2000 particle-sizing instrument (Malvern Instruments, Worcestershire, UK). Soil pH was measured on air-dried soils with a pH meter, in a 1:2.5 mass: volume soil and water suspension. The microbial biomass C (MBC) and N (MBN) were measured on field moist soils stored at 4°C by the chloroform fumigation extraction method (Vance, Brookes, & Jenkinson, 1987). Soil availability N was extracted with 2 M KCl to determine the exchangeable NH_4^+–N and NO_3^-–N concentrations, using a SKALAR San^{++} Analyzer (Skalar, Breda, The Netherlands). Available P was determined according to the Mehlich-3 method (Carter & Gregorich, 2006). Details of the methods are further described in Fan et al. (2018).

We also used the field moist soils stored at 4°C to investigate soil extracellular enzymes, which are known to play key roles in the mineralization of C, N and P in soils, including β-glucosidase (βG), cellobiohydrolase (CB), phenol oxidase (PHO), peroxidase (PER), N-acetylglucosaminidase (NAG) and acid phosphatase (AP-tase) (Table S1). These soil extracellular enzymes can be broadly divided into two groups: hydrolytic enzymes (βG, CB, NAG, AP) and oxidative enzymes (PHO, PER). Subsamples of the field moist soils were assayed for the potential activity of the hydrolytic enzymes and oxidation enzymes involved in C, N and P acquisition (Table S1) (Saiya-Cork, Sinsabaugh, & Zak, 2002). The details of these analyses are described in Li et al. (2018).

To derive specific enzyme activity indices, we normalized total enzyme activity by using the total potential activity by the MBC concentration. We calculated the ratios of C, N and P acquiring enzyme activities based on Sinsabaugh et al. (2008). Thus, we obtained the NAG/C_{enz}, NAG/AP-tase and C_{enz}/AP-tase as indicators of microbial nutrient acquisition (Sinsabaugh, Hill, & Follstad Shah, 2009).

2.5 | Soil CO_2 flux and its carbon-isotopic signature

The CO_2 fluxes were sampled and measured monthly from January to December in 2017 using static chambers and the gas chromatography technique (Figure S4; Karberg, Pregitzer, King, Friend, & Wood, 2005). We used a removable chamber (diameter = 20 cm, height = 22 cm) to collect gas samples from each mesocosm. To mix the air in the chamber, we installed a 10-cm-diameter battery-operated fan inside each chamber cover while the sample was collected. We used 50-ml plastic syringes to collect 30-ml gas samples every 20 min from the sealed mesocosm chambers and then injected the samples into 50-ml pre-evacuated gas bags. Simultaneously, air temperature within each experimental chamber was measured with a mercury thermometer. Soil temperature (SK-250WP, Sato Keiryoki, Kanda, Japan) and moisture (TDR300, Spectrum, Aurora, USA) were measured directly outside each mesocosm.

We measured CO_2 concentrations with gas chromatography (GC-2014, Shimadzu, Kyoto, Japan). Isotopic analyses for CO_2 were conducted with an isotope ratio mass spectrometer (Finnigan MAT-253; Thermo Electron, San Jose, CA, USA) at the Stable Isotope Mass Spectrometry Laboratory at Fujian Normal University. The stable carbon-isotopic signatures ($\delta^{13}C$) are expressed as per mil (‰), relative to the Pee Dee Belemnite (PDB) 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 $\delta^{13}C$.

To obtain the CO_2 flux derived from each mesocosm, we used linear model regression analysis of the changes in CO_2 concentration in each chamber with time over a 40-min period, and from this we obtained the slopes (i.e. CO_2 production rate) of the relationship between CO_2 concentration and time. The slope is rational when the regression coefficients >.9 (Metcalfe et al., 2007):

$$F = \Delta C/\Delta t \times 273/(273 + T) \times 44/22.4 \times V/A \quad (1)$$

where F is the CO_2 flux (mg m^{-2} hr^{-1}), T is the air temperature inside the chambers, 44 is the molecular weight of CO_2, 22.4 is the molar volume of an ideal gas at standard temperature and pressure (1 mol^{-1}), V is the chamber volume (m^3), and A is the chamber area (m^2).

2.6 | Partitioning of C sources in CO_2 and priming effect calculations

We used a two-component mixing model to evaluate the values of $\delta^{13}C$–CO_2 sampled at a series of time points (Ohlsson et al., 2005):

$$\delta C = \delta_{40}C_{40} - \delta_0 C_0 = C_{40} - C_0 \quad (2)$$

where the C_0 and C_{40} represent the CO_2 concentration at the 0- and 40-min time intervals, respectively; δ_0 and δ_{40} represent the ^{13}C values of CO_2 at the 0- and 40-min time intervals, respectively. For evaluation of the δ value, the above models were rearranged:

$$\delta = (\delta_{40}C_{40} - \delta_0 C_0)/(C_{40} - C_0) \quad (3)$$

The priming effect (PE, g C/m^2) of leaf litter addition on native SOM mineralization was defined using the following equations. The ^{13}C-labelled leaf litter allowed the separation of soil (*R*s) and leaf litter-derived C (*R*c) in the released CO_2 to be calculated using the mass balance equations (Fontaine et al., 2011):

$$Rs + Rc = Rt \quad (4)$$

$$Rs \times As^{13} + Rc \times Ac^{13} = Rt \times At^{13} \quad (5)$$

where As^{13} is the ^{13}C abundance of soil C, Ac^{13} is the ^{13}C abundance of leaf litter, Rt is the total CO_2 emitted from soil with leaf litter, and At^{13} is ^{13}C abundance measured in the CO_2 trap.

The PE induced by the addition of litter was calculated as.

$$PE = (Rs \text{ soil with litter}) - (Rs \text{ control soil}) \quad (6)$$

where Rs control soil is the CO_2 emitted by the control soil and Rs soil with litter is the CO_2 evolved from the soil treated with litter.

In addition, we determined home-field advantage (HFA) for litter decomposition and PE by calculating the HFA as the % R increase in litter-derived CO_2 and primed CO_2 at home compared to away environments for the two litter types, following Austin, Vivanco, González-Arzac, and Pérez (2014) and Di Lonardo et al. (2018):

$$HFA = (R_{home} - R_{away}) / R_{home} \times 100$$

where R_{home} and R_{away} are the litter-derived CO_2 or primed CO_2 at home and in away environment, respectively.

2.7 | Statistics analyses

A repeated ANOVA was performed to analyse the temporal effects of leaf litter addition on SOM mineralization (released CO_2) and litter decomposition. A t test was used to test the effects of elevation on soil and litter properties, MBC, MBN, N and P availability, PE and priming efficiency. Linear mixed models effect (LMME) was used to detect the effects of litter quality, elevation and their interaction effect on DOC, MBC, MBN, available N and P, litter decomposition, PE, and enzymes activity. In all statistics analyses, the five plots were considered as independent replicates, and the mesocosms (cores) nested within subplots were set as a random factor. In the fitted LMME, treatment (three levels), elevation (two levels) and their interaction terms were modelled as fixed effects, with both the plots and mesocosms within plots being modelled as random effect. The magnitude of the PE across the five plots at each of the two sites was plotted against priming efficiency, and the best fit model (an exponential fit) was chosen to describe their mutual relationship. All statistical analyses were performed using the SPSS 21.0 statistical software (SPSS version 21.0, SPSS Inc., Chicago, IL, USA) at a significance level of $p < .05$. The Spearman correlation between the PE and different variables as well as between each other was calculated using the R package Corrplot (Wei, 2016). Only the correlations with p-values <.05 were considered as significant and were thus visualized.

3 | RESULTS

3.1 | Litter decomposition and priming effects

The high-quality litter mineralized faster at the low elevation site ($p < .01$), while the low-quality litter mineralized faster at the high elevation site ($p < .001$; Figure 1). The high-quality litter mineralized faster than the low-quality litter at the low elevation site, while the opposite pattern was found at the high elevation site (Figure 1). These results indicate that there was a significant site × litter quality interaction ($F = 130$, $p < .001$; Table S2). In addition, the LMME results showed that litter quality ($F = 162$, $p < .001$) had a stronger influence on litter decomposition rate than site ($F = 6.4$, $p = .022$; Table S2).

Both high- and low-quality litter additions significantly increased soil C mineralization and induced a stronger priming effect (PE, g C/m^2) at the low versus high elevation site (Figure 2a). The PE induced by high-quality versus low-quality litter was 130% and 67% higher, respectively, at the low versus high elevation site (Figure 2a). Overall, additions of high-quality litter induced a stronger PE than additions of low-quality litter. In contrast to litter decomposition rates, site ($F = 115$, $p < .001$) had a stronger influence on PE than litter quality ($F = 4.3$, $p = .055$), but there was a significant interaction between site and litter quality for PE ($F = 24$, $p = .001$; Table S2).

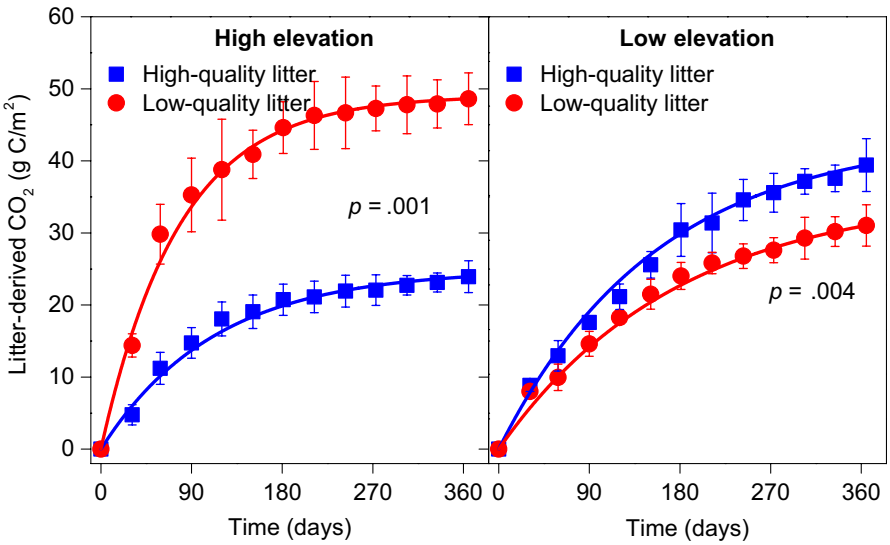

FIGURE 1 Cumulative mineralization of the high-quality and low-quality litter at the two elevations. p-values indicate significant difference between litter types within same elevation. Values represent $M \pm SD$ ($n = 5$)

The high-quality litter showed higher priming efficiency than the low-quality litter. Priming efficiency of both litter types was higher at the low versus high elevation site (Figure 2b). The PE increased exponentially with increasing priming efficiency ($p < .001$, $r^2 = .86$; Figure 3a).

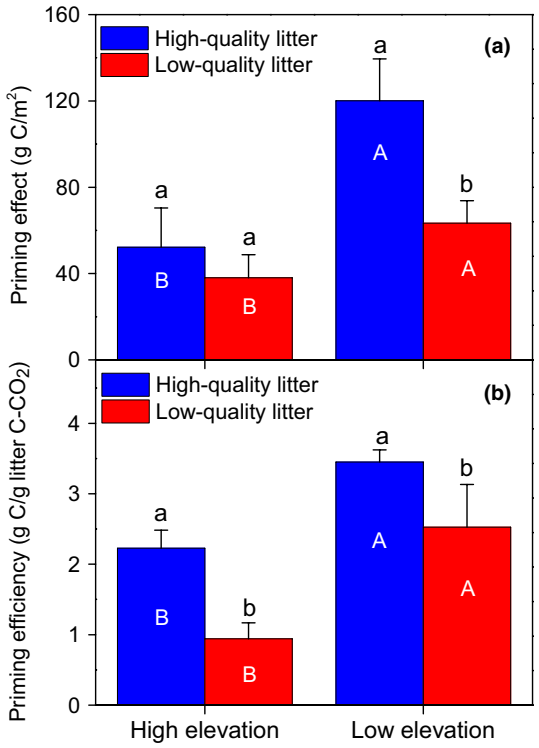

FIGURE 2 Priming effects after addition of ^{13}C labelled high- and low-quality litters (a) and priming efficiency that represents the primed C induced by per unit litter mineralized C (b) after an one-year field incubation period at the two elevation sites. Values represent $M \pm SD$ ($n = 5$). Different capital letters within bar indicate significant differences between elevations within same litter type, and different lowercase letters above bar indicate significant differences between litter types at same elevation ($p < .05$)

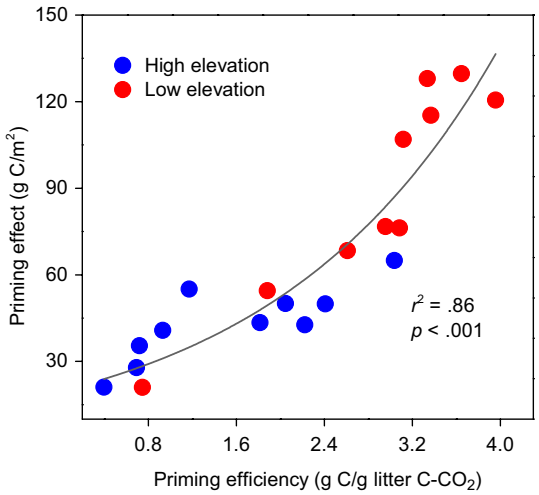

FIGURE 3 Priming effect correlated with priming efficiency. Priming efficiency was calculated using the primed soil carbon divided by the litter decomposition-derived carbon

3.2 | Home-field advantage in litter decomposition and priming effect

The HFA indexes calculated for both litter decomposition and PE were significantly different from zero (Figure 4a), and HFA for decomposition of both the high- and low-quality litter was above zero. The HFA for decomposition of low-quality litter was significantly higher than that of the high-quality litter ($p = .032$). In contrast, HFA for high-quality litter-induced PE was significantly higher than for low-quality litter. Further, the HFA for high-quality induced PE was above zero, while HFA for low-quality litter-induced PE was below zero (Figure 4a). In addition, the regression analysis showed a negatively linear relationship between litter HFA and priming HFA for both litter types ($r^2 = .66$, $p = .004$; Figure 4b).

3.3 | Microbial biomass and availability of nitrogen and phosphorous

The MBC and MBN were higher at the high versus low elevation site regardless of treatments. Neither litter type affected MBC or MBN (Table 3). Litter addition had no influence on inorganic N, dissolved

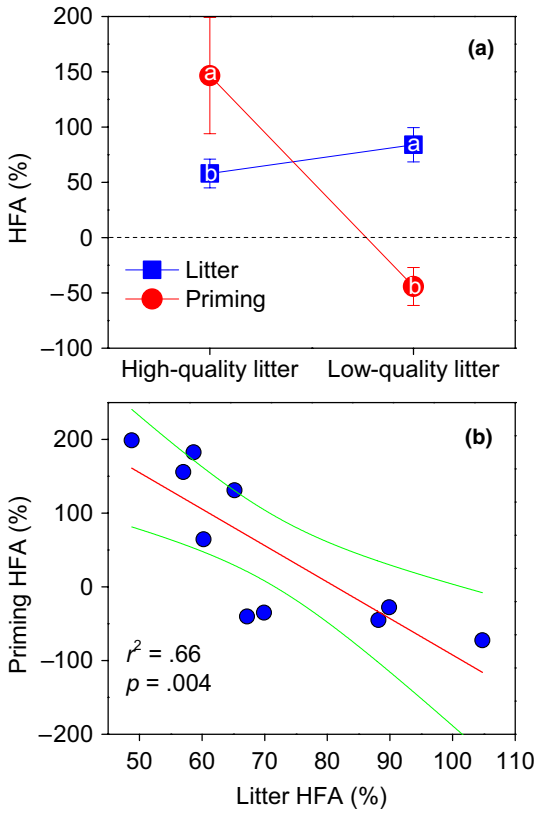

FIGURE 4 Home-field advantage (HFA) calculated as the additional decomposition at home of the cumulative litter-derived $C–CO_2$ and cumulative primed $C–CO_2$ after one year of incubation (a), relationship between litter HFA and priming HFA for both high- and low-quality litter. Values represent $M \pm SD$ ($n = 5$). Different lowercase letters indicate significant differences between high- and low-quality litter decomposition and priming effect ($p < .05$)

TABLE 3 Soil microbial biomass carbon (MBC) and nitrogen (MBN), mineral nitrogen (NH_4^+ plus NO_3^-) and available phosphorous (P), eight months after litter addition

Treatments	MBC (mg/kg)		MBN (mg/kg)		Mineral N (mg/kg)		Available P (mg/kg)	
	High elevation	Low elevation	High elevation	Low elevation	High elevation	Low elevation	High elevation	Low elevation
Control	1,229 ± 229A	534 ± 146B	138 ± 33A	79 ± 22B	38.7 ± 9.3A	28.7 ± 7.6A	3.1 ± 0.8A	1.5 ± 0.6B
High-quality litter	1,347 ± 261A	738 ± 115B	160 ± 24A	97 ± 11B	34.9 ± 7.0A	23.2 ± 3.6B	3.6 ± 0.8A	1.8 ± 0.5B
Low-quality litter	1,237 ± 109A	729 ± 88B	148 ± 14A	78 ± 17B	49.9 ± 7.6A	22.9 ± 4.3B	3.9 ± 1.5A	1.7 ± 0.6B

Note: Values represent $M \pm SD$ ($n = 5$). Different capital letters in the same rows indicate significant differences between the altitude for each variable ($p < .05$).

organic C or dissolved organic N concentrations (Table 3, Table S3). Concentrations of mineral N (NH_4^+ plus NO_3^-) were similar across high and low elevation sites under control treatment; concentrations of available P were higher for the high compared to the low elevation site across all treatments (Table 3).

3.4 | Soil extracellular enzyme activities

For C-degrading enzymes, litter addition had a negative effect on βG activity at the low elevation site, but no influence was observed at the high elevation site, and there was an interaction for βG activity between site and litter quality ($F = 5.2$, $p = .013$; Figure 5). The PHO activity at the low elevation site was higher than that at the high elevation site ($p = .05$) where there was interactive effect on PHO activity between site and litter quality ($F = 5.2$, $p = .014$). At the low elevation site, both high- and low-quality litter additions increased the PHO and PER activities compared to the control (Figure 5). For the nutrient-acquiring enzymes, there were no site or litter quality effects on the activity of N acquiring enzyme (NAE) while significant effects of site and litter quality on the activity of P acquiring enzyme (PAE) (Figure 5). The activity of PAE was significantly higher at the low elevation site, where PAE activity increased by 36% and 22% after addition of high- and low-quality litters, respectively, than at the high elevation site, where PAE activity increased by 35% and 85% after addition of high- and low-quality litters, respectively (Figure 5).

The NAE/C_{enz} at the high elevation site did not differ from that at the low elevation site; litter addition did not affect the NAE/C_{enz} at either the high or low elevation site (Table S4). The NAE/AP-tase at the high elevation site (average ratio = .11) was higher than at the low elevation site (average ratio = .05) across all treatments, while there was no litter quality influence on the NAE/AP-tase. The C_{enz}/AP-tase was higher at the high elevation site than at the low elevation site, while litter addition decreased the C_{enz}/AP at both the high and low elevation sites (Table S4).

3.5 | Correlation between priming and different variables

The correlations were plotted to explore the relationship of the PE with different variables. The PE was negatively correlated with the MBC ($p = .010$), MBN ($p = .048$), DOC ($p = .024$), mineral N ($p = .001$) and available P ($p = .008$; Figure 6). The PE showed a positive linear relationship to the C degrading (CBH, PHO and PER) and PAE activities, while no relationship to NAE activity was observed (Figure 6). There was a positive relationship between the available P and P acquiring enzyme activity ($p = .020$), but no relationship between mineral N and N acquiring enzyme activity was observed ($p = .567$; Figure 6).

4 | DISCUSSION

There has been increasing interest in understanding how litter quality and environmental variables influence the priming of SOM

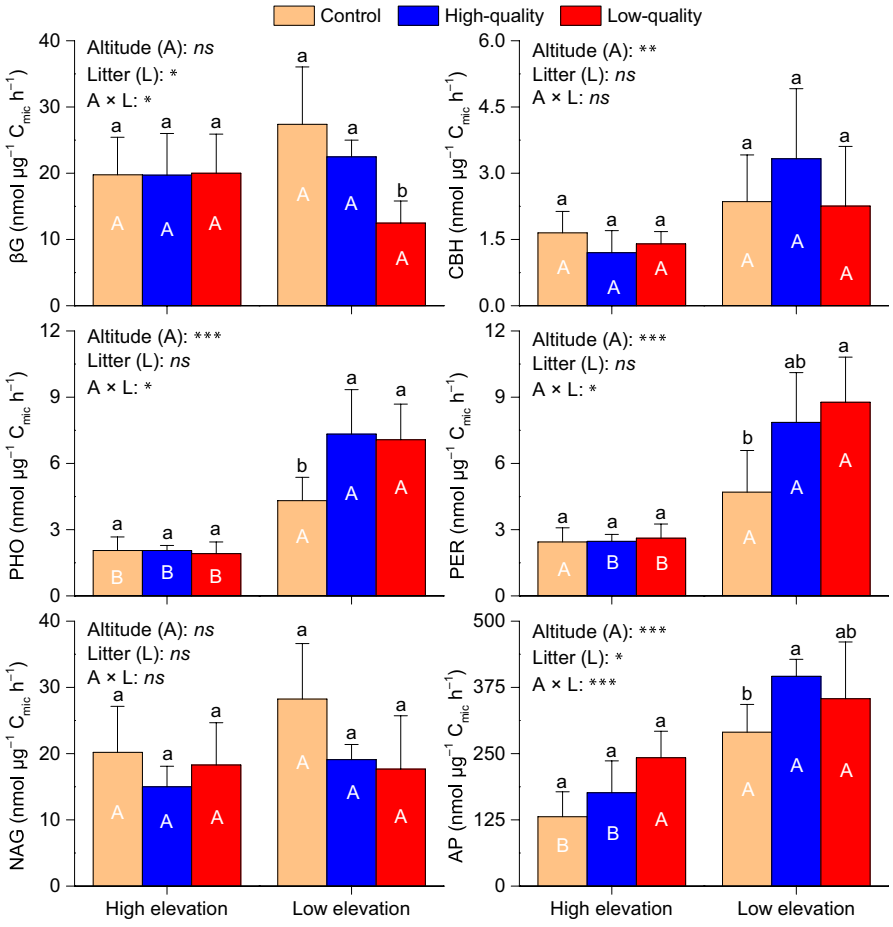

FIGURE 5 Specific potential activity of the hydrolytic and oxidative enzymes (nmol μg^{-1} C_{mic} hr^{-1}) involved in C, N and P acquisition. The values are *M* ± *SD* (*n* = 5). C_{mic}: microbial biomass C; βG: β-1, 4-glucosidase, CBH: cellobiohydrolase; PHO: phenol oxidase; PER: peroxidase; NAG: β-1, 4-N-acetylglucosaminidase; AP: acid phosphatase. Capital letters indicate significant differences between the altitudes; lowercase letters indicate significant differences among treatments within the same altitude ($p < .05$). ns, no significance; *, $p < .05$; **, $p < .01$; ***, $p < .001$

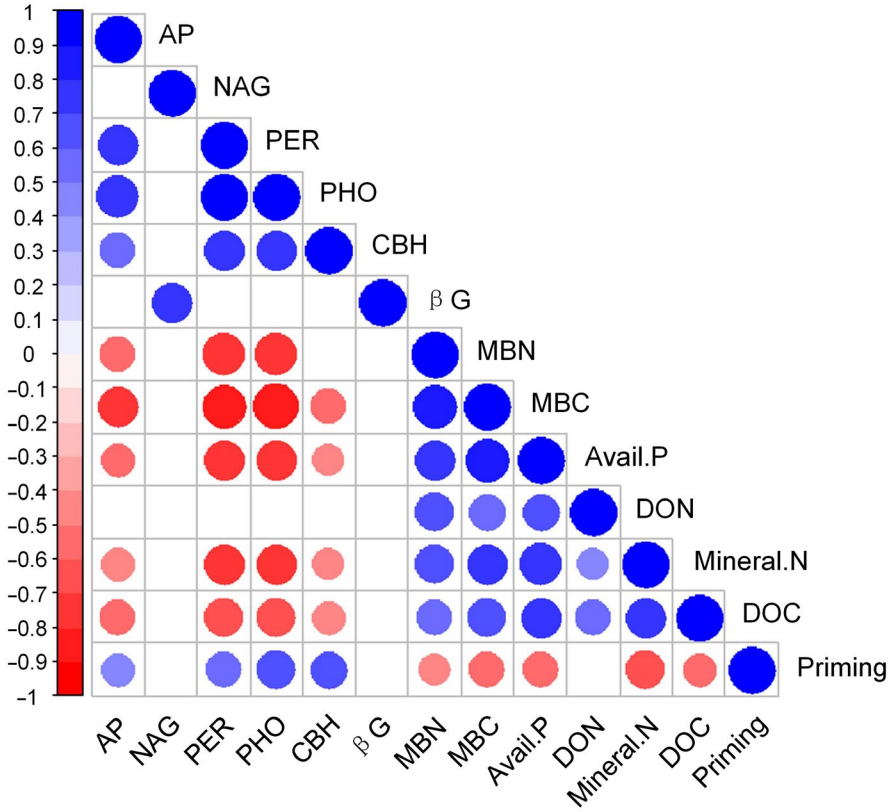

FIGURE 6 Spearman rank correlation between the priming effects and different variables. Only significant correlations ($p < .05$) are shown. Circles with blue and red colours indicate positive and negative relationships, respectively, Circle size indicates the *p*-values. Note: all the coefficient and *p*-values are shown in Figure S5

decomposition. Most studies to date have relied on laboratory incubation experiments to address questions of priming (Anderson & Hetherington, 1999; Creamer et al., 2015; Hicks et al., 2019), with few in situ studies examining PE under field conditions (Kumar, Kuzyakov, & Pausch, 2016). Results from our field study across two contrasting subtropical sites provide strong evidence that the magnitude of PE is influenced by the interaction of litter quality, site characteristics and home-field advantage. Our work further highlights the importance of understanding nutrient availability in PE studies, because litter-derived energy appears to have been used by microbes in these subtropical montane forests to synthesize AP enzyme that was used for P mining.

4.1 | Microbial nutrient mining and priming effects on SOM

Our first hypothesis about low-quality litter inducing stronger PE compared to high-quality litter (Fontaine et al., 2011) was not supported by our data. Instead, we found that high-quality litter resulted in higher PE, and this effect was stronger at the low elevation site (Figure 2). These findings point to the possibility that high-quality substrates (i.e. high N availability; low lignin or polyphenol content) exert a controlling influence over SOM decomposition rates in our study system. While they do not preclude N mining, these results conflict somewhat with the N mining hypothesis, but they do align with two laboratory studies reporting that amino acids characterized by low C/N can induce strong positive priming of SOM (Hamer & Marschner, 2005; Mason-Jones et al., 2018). Notably, the C/N of the low C/N amino acid additions varied from 1.3 (arginine) to 7.7 (phenylalanine and tyrosine), and this range in C/N did not affect PE size.

The influence of litter quality on PE is increasingly being examined from the perspective of microbial enzyme synthesis (Chen et al., 2014; Loeppmann, Blagodatskaya, Pausch, & Kuzyakov, 2016). In this study, soil N status was higher at the high elevation site compared with the low elevation site, but N acquiring enzyme activity and NAG/C_{enz} at the high elevation site were both similar to values at the low elevation site regardless of litter addition treatment. Further, there was no relationship between mineral N and NAG activity or between PE and NAG activity (Figure 6). Taken together, our results do not support our hypothesis that PE is affected by N availability. However, because soils and SOM differed across the two sites, in situ efficiency differences in NAG activity may have resulted in higher N availability in one of the sites that we could not detect. For example, we found that litterfall rates were similar between the two sites, but the low elevation site produced higher quality (higher N content litter), indicating that nutrient supply (availability) was higher at this lower elevation site. Ideally, future studies will incorporate multiple levels of litter addition rates representing a range of nutrient inputs to soil.

In contrast to N, our results show that P acquiring enzyme activity was high while NAG/AP and C_{enz}/AP were low across all treatments at both the high and low elevation sites. Compared with temperate forests, our findings are in line with P being a generally more limiting to plant growth in subtropical forests (Fan et al., 2018; Sinsabaugh et al., 2008). The higher AP-tase activity and lower NAG/AP-tase and C_{enz}/AP-tase at the low elevation site suggest a high microbial investment in P acquisition. Further, there was a negative relationship between the PE and available P and a positive relationship between the PE and AP activity, supporting the interpretation that PE in our study was regulated by microbial P mining (DeForest, 2019).

Furthermore, the C_{enz}/AP-tase and the production of C degrading enzymes relate to P acquisition and were similar across the low- and high-quality litter treatments, perhaps explaining why PE sizes induced by the high- and low-quality litter at the high elevation site were similar. Conversely, at the low elevation site, AP-tase activity increased by 36% and 22% after addition of the high- and low-quality litters, respectively, and the C_{enz}/AP of the high-quality litter treatment was higher than the low-quality litter treatment, suggesting that microbes under the high-quality litter treatment invested more C towards the acquisition of P from SOM. Taken together, these results for the low elevation site indicate that high-quality litter caused micro-organisms to decompose more native SOM to meet microbial P demands compared with low-quality litter (Halvorson et al., 2019; Rousk, Hill, & Jones, 2015).

4.2 | Home-field advantage affects litter decomposition

We found that high-quality litter decomposes more quickly at the low elevation site, in line with litter decomposition studies along temperature gradients (Bothwell, Selmants, Giardina, & Litton, 2014; Fierer, Craine, McLauchlan, & Schimel, 2005; Giardina et al., 2014; Veen et al., 2015), but low-quality litter decomposed more slowly at the low elevation than at the high elevation site, supporting our second hypothesis that HFA regulation of litter decomposition can more than offset the effects of temperature differences on litter decomposition. We suggest that the pattern we observed is based on HFA-driven microbial community preference for litter originating from the community's location, and this effect was stronger for low-quality litter.

Our results are consistent with a litter bag-based field study in the San Juan Mountains of southwest Colorado, USA, where HFA for low-quality *Pinus contorta* litter was much stronger than HFA for higher quality *Populus tremuloides* litter (Wallenstein et al., 2013). In our study, the stronger HFA for our low-quality coniferous *C. lanceolata* litter may relate to the higher abundance of fungi at the *Pinus* and *Cunninghamia* dominated high elevation site (Li et al., *unpublished data*). If this interpretation is correct, then it may be that the higher abundance of fungi at the high elevation site is more effective at utilizing the low-quality litter, resulting in a higher decomposition rate. By contrast, *C. carlesii* dominated forests at the low elevation site supported a microbial community tuned to the decomposition of high-quality *C. carlesii* litter. The stronger HFA for low versus high-quality litter may indicate that the decomposition of *C. lanceolata* litter results from a microbial community that includes specialists for that litter type, but that these specialists were less abundant at the low elevation site. In contrast, decomposition of the high-quality *C. carlesii* litter proceeded at both sites

with low elevation specialists having smaller advantage over high elevation specialists. Based on our observation, HFA for low-quality litter is strong enough to override widely documented temperature responses, but the HFA decomposition of high-quality litter is weaker and unable to override the effect of temperature on decomposition (Craine, Fierer, & McLauchlan, 2010).

4.3 | Relationship between litter decomposition and priming effect

In contrast to previous research showing a stronger HFA for litter decomposition translates into a stronger HFA for PE (Di Lonardo et al., 2018), we found a negative relationship between litter HFA and priming HFA (Figure 4b). As a result, a specialized litter decomposer community driving HFA cannot be assumed to become more effective at decomposing SOM following additions of litter. This lack of correspondence between low-quality litter could be explained by the microbial substrate preference utilization hypothesis, whereby micro-organisms switch to decomposing litter for energy and nutrients versus SOM (Lyu et al., 2018). While we observed no litter type differences in PE at the high elevation site, high-quality litter induced a stronger PE compared with low-quality litter at the low elevation site. Further, these results appear to support our third hypothesis that PE induced by high-quality litter would appear to be more sensitive to temperature differences than PE induced by the low-quality litter; these findings are perhaps better explained by the important influence of HFA at the coniferous tree dominated high elevation site but the weaker HFA for high-quality litter at the broadleaf dominated low elevation site. From these results, we conclude that litter quality-based variation in HFA can drive resulting patterns for PE. Obviously then, the PE for microbial communities from sites with a narrower range of higher quality litter inputs would be more sensitive to variation in litter quality. Overall, variation in PE is probably driven by interaction of litter quality, abiotic variables and the microbial community as influenced by both HFA and preferential substrate utilization, with the interactions and influences being dynamic through time as all the contributors to observed patterns are also dynamic.

Our results also indicate that PE was influenced by microbial substrate use efficiency. We calculated priming efficiency as PE induced per unit of litter-derived CO_2–C and found a positive relationship between PE and priming efficiency, where priming efficiency resulting from high-quality litter consistently exceeded priming efficiency resulting from low-quality litter, indicating that micro-organisms mineralizing the same amount of litter-derived C could acquire more energy from the high-quality litter for decomposing native SOM to meet their nutrients demands (Lü et al., 2015; Sauvadet et al., 2018). As the easily available C sources are utilized and depleted over time, the low-quality litter would become more recalcitrant (Chao et al., 2019; Melillo, Aber, & Muratore, 1982), and so more energy would be required for microbial decomposition of litter, with less available for SOM decomposition (Blagodatskaya & Kuzyakov, 2008; Strickland, Osburn, Lauber, Fierer, & Bradford, 2009).

5 | CONCLUSIONS

Our investigation of the role of HFA, preferential substrate utilization and litter quality in litter decomposition, PE and priming efficiency in subtropical forests has led to several key findings: (a) high-quality litter addition induced greater PEs than the low-quality litter, which is inconsistent with the N mining hypothesis that low-quality litter causes greater PE than high-quality litter; (b) HFA controls on litter decomposition are sensitive to litter quality considerations, with stronger HFA when home litter quality is low; (c) high-quality litter-induced PE is more sensitive to site difference than PE induced by low-quality litter; (d) divergent PEs induced by the high- and low-quality litters are mainly regulated by the microbial metabolic efficiency and the investment of litter-derived energy for microbial P mining in subtropical forests.

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AUTHORS' CONTRIBUTIONS

This project was conceived by M.L. and Y.N. who collected the data under the supervision of J.X., Y.N., Y.R. and Z.F.; M.L. C.P.G. and M.W. analysed the data. M.L., C.P.G., M.A.V. and J.X. contributed to the writing of the manuscript. Both C.J. and X.L. have approved this manuscript for submission.

DATA AVAILABILITY STATEMENT

Data are available at the Dryad Digital Repository https://doi.org/10.5061/dryad.674g1f7 (Lyu et al., 2019).

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SUPPORTING INFORMATION

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

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