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Carbon and nitrogen inputs differentially affect priming of soil organic matter in tropical lowland and montane soils

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ABSTRACT

Microbial decomposition of soil organic matter (SOM) can be accelerated or reduced by the combined effects of carbon (C) and nutrient inputs through a phenomenon known as 'priming'. Tropical lowland and montane soils contain large stores of C and may undergo substantial future changes in C and nutrient inputs due to global change, yet how these inputs might interact to influence priming is poorly understood in these ecosystems. We addressed this question using soils from a 3400 m tropical elevation gradient which vary strongly in nitrogen (N) and phosphorus (P) availability. To determine how existing nutrient availability in different tropical soils regulates microbial activity, and whether microbial demand for nutrients leads to priming, soils were amended with simple and more complex ^{13}C-labelled substrates in combination with inorganic N, P and N + P. Isotopic partitioning (^{13}C in CO_2 and in phospholipid fatty acids; PLFA) was used to identify sources of C (substrate- or SOM-derived) in respiration and in microbial communities. Nutrient treatments did not influence the amount of substrate-respired C for any of the soils, but did affect the direction and magnitude of priming effects. For the upper montane forest and grassland soils, C addition had a relatively minor influence on the turnover of SOM, but N addition (with or without C) reduced SOM mineralisation (negative priming), suggesting reduced microbial N-mining from SOM when N was externally supplied. By contrast, in the lower montane and lowland forest soils, C addition increased SOM mineralisation (positive priming), but the response was unaffected by nutrient additions. The assimilation of ^{13}C substrates into functionally active microorganisms revealed that C substrate complexity, but not added nutrients, strongly affected C-use within the microbial community: in both lowland and montane forest soils, fungi assimilated a greater proportion of the simple C substrate, while gram-positive bacteria assimilated a greater proportion of the more complex C substrate. Overall, our results have contrasting implications for the response of soil C cycling in tropical montane and lowland ecosystems under future global change.

1. Introduction

Tropical soils are a globally important store of terrestrial carbon (C) (Jobbágy and Jackson, 2000), with soil microorganisms playing a decisive role in regulating net soil C storage through the mineralisation of plant residues and soil organic matter (SOM). Elevated concentrations of atmospheric carbon dioxide (CO_2) are expected to increase plant productivity and, in turn, inputs of plant-derived C to soil (Cusack et al., 2016). However, because C and nutrient cycles are tightly coupled according to microbial metabolic demands (Cleveland and Liptzin, 2007; Finzi et al., 2011), the availability of essential nutrients may strongly influence the response to changes in C input (Dijkstra et al., 2013; Chen et al., 2014; Carrillo et al., 2017). In the tropics, external supply of nitrogen (N) is increasing as a consequence of biomass burning (Hietz et al., 2011), with high N deposition reported even across remote Andean systems (Fabian et al., 2005; Boy et al., 2008). Aeolian sources of phosphorus (P), originating from North Africa, will also likely increase the future availability of P across the Amazon basin (Okin et al., 2004; Yu et al., 2015). Yet our ability to predict how soil C turnover will be affected by future changes to plant-derived C and nutrient supply is limited by poor understanding of the interactions between C inputs, soil nutrient availability and soil microorganisms,

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which together determine soil C dynamics in tropical ecosystems (Nottingham et al., 2015a; Homeier et al., 2017).

Microbial decomposition of SOM can be accelerated or reduced by the combined effects of plant-derived C and nutrient inputs through a phenomenon known as 'priming'. Priming effects are defined as a change to the mineralisation of SOM in response to inputs of labile C or nutrients (Kuzyakov et al., 2000; Qiao et al., 2016), resulting in either enhanced (positive priming) or reduced (negative priming) mineralisation of SOM. While several different mechanisms have been proposed to explain priming (see Blagodatskaya and Kuzyakov, 2008 for a review), responses are often strongly influenced by soil nutrient availability and microbial nutrient demand (Dijkstra et al., 2013; Chen et al., 2014). For example, soil nutrient stoichiometry was found to be the strongest driver of different priming effects in a recent study of temperate grassland soils (Carrillo et al., 2017). In soils where nutrient availability is low, inputs of labile C may be used as a source of energy to support microbial activity, with microorganisms co-mineralising SOM (positive priming) to liberate and acquire 'limiting' nutrients from soil (nutrient-mining) (Craine et al., 2007; Murphy et al., 2015; Meier et al., 2017). Conversely, negative priming may occur in response to labile nutrient inputs, due to reduced mining of SOM for nutrient acquisition (Janssens et al., 2010; Bird et al., 2011; Poeplau et al., 2016; Tian et al., 2016). However, previous studies have primarily focused on how N availability influences priming, with little consideration for the role of P, which could be more limiting in many tropical soils (Camenzind et al., 2017).

The different sources from which N and P are derived in terrestrial ecosystems – N from the atmosphere and P from bedrock – means that strongly weathered tropical lowland soils may be more deficient in P (Walker and Syers, 1976; Reed et al., 2011). By contrast, younger montane forest and grassland soils may be more deficient in N, because of slow rates of decomposition and biological N-fixation (due to cooler temperatures; Tanner et al., 1998), while P remains abundant due to bedrock turnover (e.g. landslide events) and near-surface weathering (Porder et al., 2007). Fertilisation with N and P, in different montane and lowland forests respectively, has been shown to increase decomposition rates (Cleveland et al., 2002; Kaspari et al., 2008; Fisher et al., 2013; Camenzind et al., 2017). A change in investment into nutrient acquisition by soil microorganisms has also been identified along a forested elevation gradient in Peru, suggesting a shift with elevation in the relative demand for P and N by microbes (Nottingham et al., 2015b). Priming may therefore occur due to microbial demand for N in tropical montane soils and P in lowland soils.

Nutrient availability may also influence the relative abundance of different microbial functional groups, which can in turn influence priming (Nottingham et al., 2009; Fontaine et al., 2011; Rousk et al., 2016). Some tropical and temperate studies have shown that fungi are more limited by N-availability (Liu et al., 2013; Fanin et al., 2015a; Nottingham et al., 2018), whereas bacteria are more constrained by P-availability (Güsewell and Gessner, 2009; Fanin et al., 2015b). However, a recent meta-analysis suggested that N addition typically reduces fungal biomass and increases bacterial biomass (Zhou et al., 2017). Microbial community composition, mediated by the availability of N and P, may have important implications for soil C turnover (Ramirez et al., 2012), as different microbial functional groups have been attributed to the mineralisation of labile and more recalcitrant sources of C (Waldrop and Firestone, 2004; Brant et al., 2006). For example, in one tropical study, increased bacterial abundance facilitated the mineralisation of labile C compounds, whereas fungal growth was associated with the mineralisation of more recalcitrant soil C fractions (Cusack et al., 2011a). Taken together, these findings suggest that mineralisation of more complex C substrates and recalcitrant SOM – primarily by fungi – may be dependent on N-availability whereas mineralisation of more labile C substrates – by bacteria – could be more dependent on P-availability. However, few studies have tested this directly (e.g. Fanin et al., 2015a).

Here we investigated the nutrient control of soil C turnover and implications for soil C stocks by examining soils along a 3400 m tropical elevation gradient in the Peruvian Andes, which vary strongly in nutrient status with elevation (Nottingham et al., 2015b). Lowland and montane soils were amended with simple and more complex ^{13}C-labelled substrates (as surrogates of plant-derived C) in combination with inorganic nutrient treatments (+N, +P, +NP). We first assessed whether nutrient amendments stimulated microbial mineralisation of added C substrates, and whether responses to N and P addition differed with elevation. We then examined whether microbial demand for nutrients resulted in priming effects, hypothesising that the addition of C substrates alone would stimulate positive priming of SOM if microorganisms co-metabolised existing SOM to meet nutrient demands, whereas C supplied with a 'limiting' nutrient would induce negligible or negative priming, due to reduced nutrient-mining. Finally, we evaluated whether bacteria and fungi were differentially constrained by N and P supply, and, if so, the consequences for mineralisation of simple and more complex C sources.

2. Materials and method

2.1. Study sites and field sampling

Soils were sampled from four sites along a 3400 m tropical elevation gradient located on the eastern flank of the Peruvian Andes (Table 1; http://www.andesconservation.org). The three highest elevation sites (3644 m, 3025 m and 1500 m above sea level; asl) are located in or close to the Manu National Park, centred on the Kosñipata Valley. The lowest elevation site (210 m) is in the Tambopata Reserve in the lowland Amazon basin, approximately 240 km east of the site at 1500 m asl. The upper three sites are separated by approximately 35 km. All sites from lowland Amazonian rainforest to upper montane cloud forest have continuous forest cover, with montane grassland occurring above the treeline at approximately 3500 m asl.

Soil fertility and microbial community composition change distinctly with elevation along the gradient. Briefly, total C, N and P in soils, and their ratios (C:N, C:P, N:P), generally increase with elevation (Nottingham et al., 2015b). Extractable inorganic P (PO_4-P) also increases with elevation, whereas mineralised N (NH_4 + NO_3) decreases with increasing elevation across the gradient (Nottingham et al.,

Table 1
Summary of site characteristics (Quesada et al., 2010; Rapp and Silman, 2012; Oliveras et al., 2014; Asner et al., 2017) and organic soil properties (reported as mean (1SE) where n = 4 from 4 subplots at each elevation site).
Mean annual temperature; MAT, mean annual precipitation; MAP, water holding capacity; WHC.

		Elevation (m asl)	MAT (°C)	MAP (mm yr^{-1})	Soil Classification	Depth Organic Layer (cm)	Organic matter (%)	80% Max. WHC (g H_2O g^{-1} fwt soil)
Tres Cruces	Montane grassland	3644	6.5	*760	Umbrisol	2.7 (0.2)	51.4 (1.6)	0.73
Wayqecha	Upper montane forest	3025	11.8	1560	Umbrisol	13.3 (1.2)	91.2 (1.4)	0.74
San Pedro	Lower montane forest	1500	18.8	5302	Cambisol	6.0 (0.4)	69.0 (6.1)	0.69
Tambopata	Lowland forest	210	24.4	1900	Haplic Cambisol	1.5 (0.3)	28.7 (3.2)	0.55

*MAP at 3450 m asl

2015b). Microbial abundance and the ratio of fungi to bacteria in soils increases with elevation, while the ratio of gram-positive to gram-negative bacteria decreases with elevation (Whitaker et al., 2014b).

Soils were sampled from four sites across the elevation gradient over one week in January 2015. Organic soil was collected from four subplots located at the corners outside the perimeter of 1 ha permanent study plots at each elevation site, resulting in a distance of at least 100 m between each sampling point, such that soil from these subplots were used as four independent replicates. Soil from the organic layer was used to enable comparison among different elevations which vary markedly in the depth of the organic horizon (Table 1). In the field, the litter layer was first carefully removed, before the organic horizon was visually determined and soil was sampled. Soils were transported in sealed plastic bags to the laboratory (Lancaster, UK) and refrigerated at 4 °C for a maximum of 4 weeks between collection and the start of the experiment.

2.2. Soil analyses

Soil from each subplot was homogenised manually by hand, and stones, woody debris, coarse roots and un-decomposed leaf fragments were removed. Soil subsamples were used to measure gravimetric water content (soil oven-dried to constant mass at 105 °C) and pH in water (soil: H_2O, 1:2.5 w:v, Hanna Instruments, USA). Organic matter content was estimated from mass loss on ignition, by heating dried and ground subsamples at 500 °C for 8 h in a muffle furnace. Dried (60 °C until constant mass) and ground soil subsamples were used to measure total C and N concentrations, using a TruSpec CN elemental analyser (LECO, USA). Total P concentration was measured using a modified dry ash procedure (Enders and Lehmann, 2012) with sulphuric acid-hydrogen peroxide digestion followed by phosphate detection by automated molybdate colorimetric analysis (Bran Luebbe AA3 Autoanalyser, Germany).

Maximum water holding capacity (WHC) was measured using composite samples of soils from each elevation site (homogenised composite of soil from four subplots from each elevation). Soils were saturated with deionised water and left to drain for 6 h in a fully humid airspace, before drying at 105 °C to constant mass to calculate water content (Öhlinger and Kandeler, 1996). Soil moisture content was standardised across soils to 80% maximum WHC (by addition of sterile de-ionised water where necessary, allowing for later addition of C and nutrient treatments in 400 µl + 400 µl solution per assay), chosen so that microbial respiration was not constrained by very high or low soil water content.

2.3. Amendment of soils with ^{13}C-labelled substrates and labile nutrients

To determine if soil nutrient availability influenced microbial mineralisation of fresh C substrates and priming of pre-existing SOM, soils were amended with ^{13}C-labelled xylose or hemicellulose in combination with three inorganic nutrient treatments (N, P, NP), plus controls, in a fully factorial design. Xylose and hemicellulose were selected as two ecologically relevant C substrates which differ in their chemical complexity; xylose represents a simple C substrate (monosaccharide, building block for hemicellulose) and hemicellulose a more complex molecule (polysaccharide, constituent of plant cell walls).

^{13}C-labelled xylose (Sigma-Aldrich, UK) and hemicellulose (IsoLife, The Netherlands) of 10.8 atom% enrichment were created by mixing uniformly labelled ^{13}C-substrates (where ^{13}C was evenly distributed across the C molecule) with equivalent non-labelled substrates. Carbon substrates were added at a concentration of 200 µg C g^{-1} fwt soil, equivalent to 0.2–0.3% of total C in the soils (Table 2). This dose rate was chosen based upon previous experimental findings, whereby this amount of added C equated to 53–100% of initial microbial biomass C (Whitaker et al., 2014b), such that microbial activity and respiration would be stimulated by the added substrate without inducing a significant increase in microbial growth (Blagodatskaya and Kuzyakov, 2008). Xylose and hemicellulose treatments were prepared by dilution in sterile deionised water so that each substrate was added in 400 µl solution per assay. As hemicellulose is insoluble, it was diluted into suspension by sonication and vortexed for 5 s prior to addition to soils.

Three inorganic nutrient treatments (N, P and NP) were included in the experiment. Nitrogen was added as ammonium nitrate (NH_4-NO_3), phosphorus as monosodium phosphate (NaH_2PO_4) and a combined N + P treatment where ammonium nitrate and monosodium phosphate were added in solution together. The concentration of these nutrient treatments was determined in order to correspond to mean C:N:P stoichiometry of soil microbial biomass (60:7:1) which is reported to be tightly constrained at a global scale (Cleveland and Liptzin, 2007). Hence, soils were amended with N and P treatments in a fixed ratio with the added C substrate (200 µg C g^{-1} fwt soil), with C:N ratio of 60:7 (equivalent to 20 µg N g^{-1} fwt soil) and C:P ratio of 60:2 (equivalent to 7 µg P g^{-1} fwt soil). Phosphorus was added in excess of C:P ratio 60:1, to account for P-sorption to clay minerals. Nutrient treatments were prepared by dissolving into sterile deionised water so that each treatment was added in 400 µl solution per assay.

Prior to the start of the experiment, soils were pre-incubated in the dark at 16.0 °C (chosen as the average mean annual temperature of the four soils used in the experiment; Table 1) for 24 h to allow equilibration to the experimental incubation temperature. One common incubation temperature was chosen in order to focus on treatment differences among soils. Aliquots of 8.0 g fwt soil were weighed into 160 ml glass Wheaton bottles (Wheaton Science Products, USA). Soils were amended with one of the ^{13}C-labelled substrates (xylose, hemicellulose or control) in combination with one of the nutrient treatments (N, P, NP, or control), with four replicates per treatment. For controls, sterile deionised water was added in place of C and/or nutrient treatments. The headspace of each bottle was flushed with compressed air for 1 min to achieve a standard starting atmosphere before bottles were sealed with butyl rubber stoppers and aluminium crimp caps. Bottles were over-pressurised by injecting 20 ml compressed air, to partly compensate for subsequent headspace gas sampling, and incubated at 16.0 °C in the dark for 7 days. In total, 192 soil assays were incubated. As soils were contained in sealed Wheaton bottles, soil moisture was maintained throughout the study, without need for additional adjustment.

Samples of compressed air were taken to measure the starting gas concentration, at time 0. To determine the evolution of CO_2 and its ^{13}C-enrichment, two headspace gas samples were taken from each bottle at 3 time points (24 h, 48 h and 168 h after C substrate-nutrient addition) by taking 5 ml gas samples with an air-tight syringe and injecting into 3 ml evacuated exetainer vials (Labco, UK). After 7 days, at the end of the experiment, soils were frozen at −80 °C and freeze dried for analysis of phospholipid fatty acid (PLFA) biomarkers. Responses measured therefore reflected short-term responses to altered C and nutrient supply.

2.3.1. CO_2 and ^{13}C-CO_2 analyses

The concentration of CO_2 in gas samples was determined using a PerkinElmer Autosystem Gas Chromatograph (GC; PerkinElmer, USA) fitted with a flame ionization detector containing a methaniser, with results calibrated against certified gas standards (BOC Ltd. Guildford, UK). Carbon dioxide fluxes were calculated using the linear accumulation of CO_2 concentrations in headspace gas samples from 0, 24, 48 and 168 h, using the approach described by Holland et al. (1999). Linear fluxes best described the data, whereby the Pearson coefficient for accumulation of CO_2 with time was greater than 0.95 for each bottle. The total CO_2 flux was calculated on a soil C mass basis (CO_2-C µg g^{-1} soil C), to normalise for differences in C content among soils.

δ^{13}C values of CO_2 were measured by isotope ratio mass spectrometry (IR-MS) using a Trace-Gas Preconcentrator coupled to an Isoprime isotope ratio mass spectrometer (IRMS, Elementar, UK).

Table 2
Soil properties (organic soil), reported as mean (1SE) where $n = 4$ from 4 subplots at each elevation site.

	Elevation (m asl)	Soil pH	Total C (mg g^{-1})	Total N (mg g^{-1})	Total P (mg g^{-1})	C:N	C:P	N:P	*Extractable PO_4-P (mg P kg^{-1})	*Mineralised N	
										NH_4-N (μg N g^{-1} d^{-1})	NO_3-N (μg N g^{-1} d^{-1})
Tres Cruces	3644	4.9 (0.1)	237 (7)	16 (0.5)	0.85 (0.03)	14.6 (0.2)	282 (15.1)	19.3 (1.0)	2.5 (0.5)	10.5 (0.8)	0.2 (0.03)
Wayqecha	3025	3.9 (0.1)	477 (10)	23 (0.7)	0.81 (0.03)	21.0 (0.8)	591 (19.2)	28.3 (1.2)	82.0 (23.3)	11.9 (0.9)	0.5 (0.2)
San Pedro	1500	3.8 (0.1)	339 (36)	23 (1.3)	1.34 (0.13)	14.5 (0.8)	268 (57.0)	18.1 (2.8)	44.7 (20.1)	13.1 (0.7)	14.1 (3.2)
Tambopata	210	3.6 (0.1)	133 (11)	7 (0.6)	0.11 (0.05)	17.9 (1.0)	491 (110)	27.4 (5.4)	2.7 (0.2)	3.4 (0.5)	24.2 (2.9)

* Determined previously (soil 0–10 cm depth) by Nottingham et al. (2015b and unpublished data for Tres Cruces). Data represent mean (1SE; $n = 5$).

Between 5 and 60 μl gas samples were manually introduced into the injection port of the pre-concentrator using a gas-tight syringe. Water was eliminated via a perchlorate chemical trap and the CO_2 cryogenically pre-concentrated by liquid nitrogen prior to gas chromatography column separation and introduction to the Isoprime IRMS via an open split. The resultant $^{13}C/^{12}C$ isotope ratios were compared to pulses of known reference CO_2 (BOC, UK) calibrated against certified reference CO_2 (NIST RM8562 CO_2- Heavy, RM8563 CO_2-Light and RM8564 CO_2-Biogenic) to determine $\delta^{13}C$ values of CO_2.

2.3.2. PLFA and ^{13}C-PLFA analyses

Microbial community composition was determined by analysis of PLFA biomarkers extracted from soils after the 7-day experimental period. The number of samples extracted for PLFAs was rationalised due to the time and resource intensity of these measurements. Hence, upper montane (Wayqecha; 3025 m asl) and lowland (Tambopata; 210 m asl) forest soils which had been amended with xylose plus N/P/control and with hemicellulose plus N/P/control were selected, to identify how the addition of N or P affected the assimilation of simple and more complex C substrates by different microbial functional groups. From these assays, three out of four replicate soils were chosen randomly. Untreated control soils (no added C, no added nutrient treatment) were also extracted for microbial PLFAs to determine the natural abundance of ^{13}C-PLFA in the soils.

Phospholipids were extracted as part of the total lipid extract from 0.50 g freeze-dried and ground soil samples by a Bligh-Dyer extraction, consisting of chloroform, methanol and 0.15 M citrate buffer (1:2:0.8, v/v/v) (Frostegård et al., 1993). The lipid containing phase was fractionated using un-bonded silica columns (ISOLUTE SI, Biotage, Sweden), with chloroform, acetone and methanol used to elute the neutral lipids, glycolipids and polar phospholipids, respectively. Methyl nonadecanoate (C19:0 Sigma Aldrich, UK) was added as an internal standard before the phospholipid samples were subjected to mild alkaline methanolysis. The resulting fatty acid methyl esters were separated and identified by gas chromatography-mass spectrometry (GC-MS) using an Agilent Technologies 5973 Mass Selective Detector coupled to an Agilent Technologies 6890 GC. Concentrations of identified PLFAs were determined via the C19:0 internal standard.

Gram-positive bacteria (GP bacteria), gram-negative bacteria (GN bacteria) and fungi (F) were identified by specific biomarkers indicative of these functional groups. Gram-positive bacteria were identified by the terminal and mid-chain branched fatty acids i15:0, a15:0, i16:0, i17:0, a17:0, GN bacteria by cyclopropyl saturated cy17:0 and cy19:0 and monosaturated 16:1ω7 and 18:1ω7 fatty acids, and saprotrophic fungi by polyunsaturated 18:2ω6,9 and monounsaturated 18:1ω9 fatty acids (Ruess and Chamberlain, 2010). Although the 18:1ω9 marker can also be present in bacteria, here the 18:1ω9 and 18:2ω6,9 markers were strongly correlated (Spearman's coefficient = 0.83, $p < 0.001$, $n = 42$), and as such both markers were used to indicate fungal abundance. The total concentration of PLFAs (μg PLFA g^{-1} dwt soil) in samples were calculated from all identified PLFAs (14:0, 15:0, 16:0, 16:1, 16:1ω5, 17:0, 17:1ω8, 10Me17:0, 17:1ω7, 18:0, 10Me18:0 and 18:1ω5), in addition to those listed above as biomarkers for fungi and bacteria.

$\delta^{13}C$ values of individual PLFAs were analysed using gas chromatography-combustion-isotope ratio mass spectrometry (GC-C-IRMS; Isoprime Ltd, UK). A sample of the methanol used for PLFA extractions was measured by continuous flow-elemental analyser-IRMS (CF-EA-IRMS), to determine its $\delta^{13}C$ value which was used to back-correct the PLFA $\delta^{13}C$ values for the addition of the extra C atom introduced to the molecule during methylation (Jones et al., 1991; see ^{13}C-PLFA calculations).

2.4. Stable isotope calculations

Enrichment of ^{13}C in CO_2 and PLFAs were expressed in delta notation, i.e. $\delta^{13}C$ (Eq. (1)), where R represents the $^{13}C/^{12}C$ ratio in the sample relative to the standard (Coleman, 2012).

$$\delta^{13}\mathbf{C}\ (‰) = \left[\left(\frac{\mathbf{R_{sample}}}{\mathbf{R_{standard}}}\right) - 1\right] \times 1000 \quad (1)$$

2.4.1. ^{13}C-CO_2 calculations

The percentage of respired CO_2 from added C substrates was calculated for treated soils at 24, 48 and 168 h, according to equation (2), derived from a mixing model. δC is the $\delta^{13}C$ value from the soil source, determined from Keeling plots as the intercept ($x = 0$) of the linear regression between $1/CO_2$ concentration and $\delta^{13}C$ (for untreated control soils, no added C or nutrient treatment). δL is the $\delta^{13}C$ value of the labelled C-substrate (10.8 atom% ^{13}C enrichment, δL = 9774.6), and δT is the $\delta^{13}C$ value of respired CO_2 from treated soils at each time point. These data were used to calculate cumulative substrate-derived C (μg CO_2-C g^{-1} soil C) respired after 24, 48 and 168 h for all soil/C substrate/nutrient treatments.

$$\%\ \mathbf{C\ substrate\ derived} = \frac{\delta\mathbf{C} - \delta\mathbf{T}}{\delta\mathbf{C} - \delta\mathbf{L}} \times 100 \quad (2)$$

The change in mineralisation of pre-existing SOM following the addition of C substrates and nutrient treatments (hereafter referred to as primed C) was calculated using a mass balance approach. Primed C (μg CO_2-C g^{-1} soil C) was estimated from total measured respiration in treated soils, minus substrate-derived respiration, minus basal respiration (from control untreated soils). For soils which were only amended with nutrient treatments (no added C substrate), the change in mineralisation of SOM (hereafter also referred to as primed C) was calculated as total measured respiration in treated soils minus basal respiration (from control soils). Primed C could be positive or negative, where positive priming represented increased mineralisation of pre-existing SOM following the addition of C substrates and/or nutrient treatments and negative priming represented reduced mineralisation of pre-existing SOM following the addition of C substrates and/or nutrient treatments.

2.4.2. ^{13}C-PLFA calculations

Isotopic enrichment of individual PLFAs were expressed as $\delta^{13}C_{PLFA}$ values after correction for the methyl-group added during methanolysis

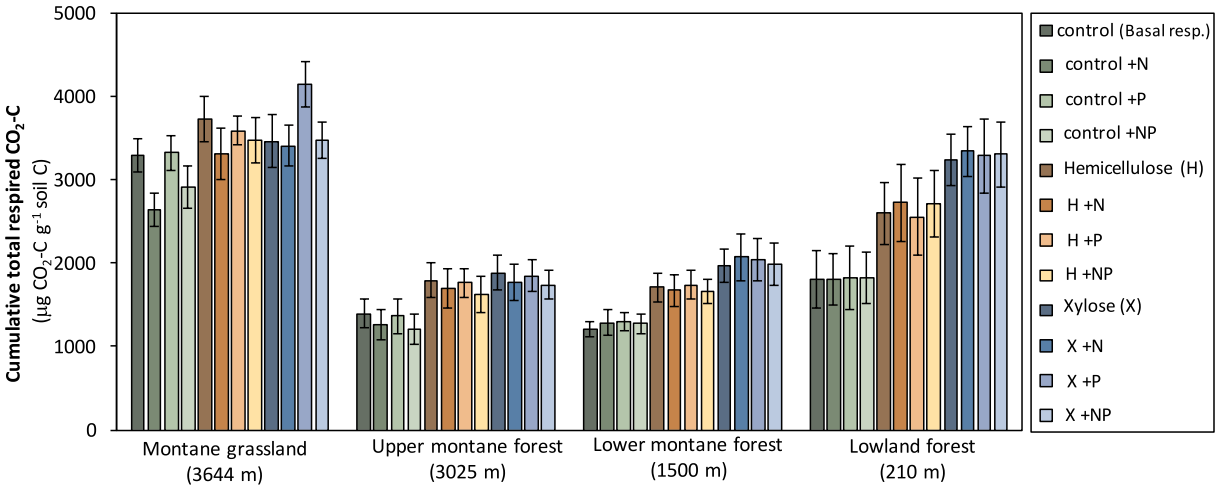

Fig. 1. Effect of C substrates (no added C (control), hemicellulose (H) and xylose (X)) in combination with nutrient treatments (no added nutrient, +N, +P, +NP) on cumulative total respired CO_2-C (µg g^{-1} soil C) from four soils incubated for 168 h at standard temperature (16 °C) and moisture (80% water holding capacity). Bars represent mean ± 1SE (n = 4).

(Eq. (3)), where nPLFA is the number of C-atoms of the PLFA molecule, $\delta^{13}C_{FAME}$ is the $\delta^{13}C$ value of the FAME after methylation and $\delta^{13}C_{MeOH}$ is the $\delta^{13}C$ value of the methanol used for methanolysis ($\delta^{13}C = -54.15‰$).

$$\delta^{13}\mathbf{C_{PLFA}} = \frac{[(\mathbf{nPLFA}+1)\delta^{13}\mathbf{C_{FAME}} - \delta^{13}\mathbf{C_{MeOH}}]}{\mathbf{nPLFA}} \quad (3)$$

To determine the assimilation of added C substrates by different microbial functional groups, the percentage of substrate-derived C within individual PLFAs was calculated by a modified version of equation (2), multiplied by the abundance of the specific PLFA (µg PLFA-C g^{-1} dwt soil) (Nottingham et al., 2009), where δC is the $\delta^{13}C$-PLFA value from untreated control soils, δL is the $\delta^{13}C$ value of the labelled substrate (as above), and δT is the $\delta^{13}C$-PLFA value from treated soils. These data were used to calculate the incorporation of the added substrate-C into individual PLFAs, from which the total C substrate incorporation into all PLFAs (µg substrate-derived PLFA-C g^{-1} soil dwt) was determined. The proportional substrate incorporation (% substrate-derived C) into different microbial functional groups (F, GP bacteria, GN bacteria, and unspecified PLFAs) were also calculated, as a percentage of the total C-substrate incorporated into all PLFAs. While it was not possible to determine an absolute value for microbial carbon use efficiency (CUE), here we calculated an index of substrate-CUE as the total substrate-derived C incorporated into PLFAs (used for growth) relative to the total substrate-derived C consumed (substrate-C incorporated in PLFAs + substrate-C respired) (Whitaker et al., 2014a), to screen for differences in the CUE of added substrates between soils and with nutrient treatments. Finally, to examine the incorporation of soil-derived C by different microbial functional groups in response to C and nutrient treatments, concentrations of excess soil-derived C in PLFAs (µg soil C g^{-1} soil) were determined by a mass balance approach, as the total concentration of PLFA-C in treated soils, minus PLFA-C in untreated control soils, minus substrate-derived PLFA-C (Nottingham et al., 2009). Positive excess soil-derived C in PLFAs represented increased assimilation of C from SOM and negative excess soil-derived C represented reduced assimilation of C from SOM, relative to untreated control soils.

2.5. Data analysis

Statistical analyses were performed using R, version 3.2.1 (R Core Team, 2015). Main and two-way interactive effects of 'Soil', 'C Substrate' and 'Nutrient Treatment' on total respired CO_2, substrate-respired C and primed C were tested by analysis of variance (ANOVA). To assess if the availability of N and P affected the assimilation of C substrates by different microbial functional groups, main and two-way interactive effects of 'Soil', 'C Substrate' and 'Nutrient Treatment' on microbial incorporation of C-substrates were also tested by ANOVA. Data analysed included total substrate-C incorporation into all PLFAs (µg substrate-derived PLFA-C g^{-1} soil dwt), the index of microbial substrate-CUE, and the relative proportion (as % of total incorporated) of substrate C incorporated into fungi, GP and GN bacteria. To meet the assumptions of ANOVA, prior to analysis, dependent response variables were first tested for normality and homogeneity of variance and transformed where necessary. Pair-wise comparisons of significant effects were conducted using Tukey's HSD post-hoc tests, with significant differences identified where $p < 0.05$.

3. Results

3.1. Soil properties

Total C, N and P (organic horizon) was lowest in the lowland forest soil (Table 2). The montane forest soils (1500 m and 3025 m) had the greatest concentration of total N (23 mg g^{-1}), while the lower montane forest soil had the greatest concentration of total P (1.34 mg g^{-1}). The concentration of total N and P in these soils does not however directly correspond to the availability of inorganic N and P. Extractable inorganic PO_4-P was low in the lowland forest soil, and typically increased with increasing elevation, but was also very low in the montane grassland soil (Nottingham et al., 2015b). Conversely, mineralised N (NH_4 + NO_3) determined by in-situ ion-exchange resins was higher in soils from the lowland and lower montane forest, compared to soils from the upper montane forest and montane grassland (Nottingham et al., 2015b, Table 2). Soil pH did not vary markedly among soils from the three forest sites (pH 3.6–3.9) but was higher in the montane grassland soil (pH 4.9).

3.2. Microbial mineralisation of ^{13}C substrates and priming of SOM

Basal respiration (CO_2 flux in the absence of added C and nutrient treatments), under controlled temperature and soil moisture, varied 2.7-fold among soils when compared on a soil C mass basis (Fig. 1). Total respired CO_2 varied among soils and C substrate treatments with a significant 'Soil x C Substrate' interaction (Supplementary Table S1). Post-hoc tests revealed that, typically, respired CO_2 was significantly greater following amendment with xylose compared to un-amended (no added C) soils (Supplementary Table S2). The exception was soil from

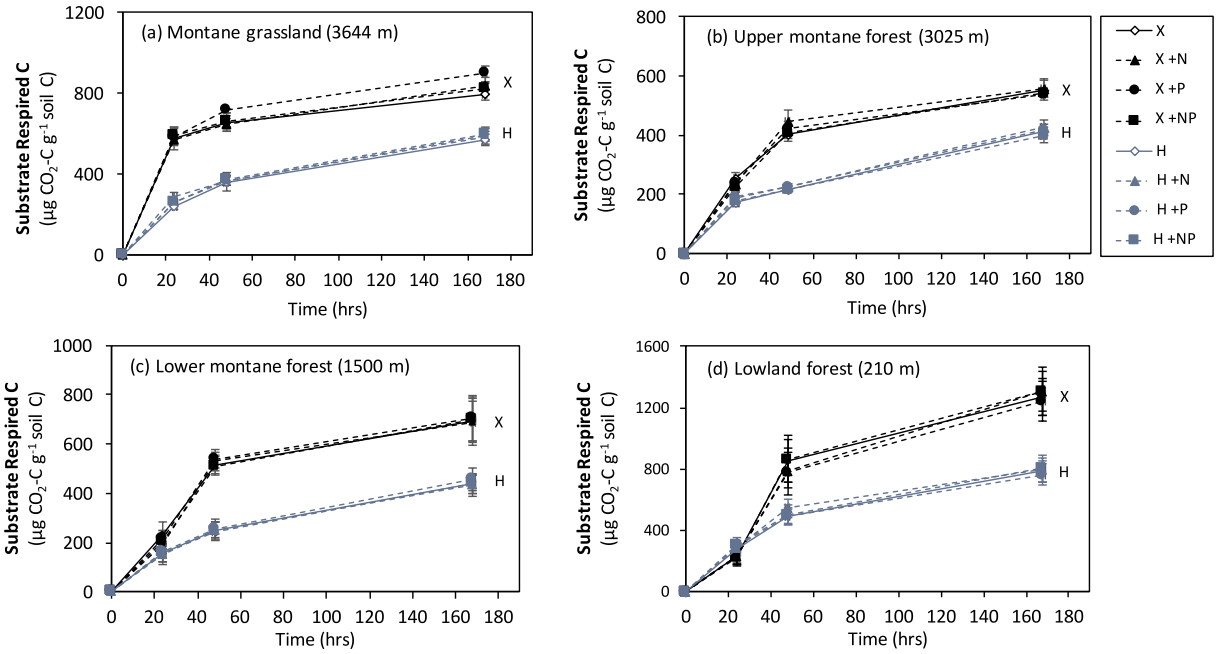

Fig. 2. Cumulative substrate respired C (µg CO_2-C g^{-1} soil C) from (**a**) montane grassland, (**b**) upper montane forest, (**c**) lower montane forest and (**d**) lowland forest soils over 168 h following amendment with C substrates (xylose (X) and hemicellulose (H)) in combination with nutrient treatments (control, +N, +P, +NP). Data represent mean ± 1SE (n = 4). Note differences in y-axis scales among panels a–d.

the montane grassland (3644 m), where there was no significant difference among un-amended and xylose-amended soils (Fig. 1). Respired CO_2 from the lowland forest (210 m) soil amended with hemicellulose was also significantly greater compared to un-amended soil, but this relationship did not hold for the other soils.

Total respired CO_2-C was partitioned into that derived from added C substrates (substrate C) and from the mineralisation of pre-existing SOM (primed C). The cumulative amount of substrate-derived C respired after 168 h varied among soils and C substrates, with a significant 'Soil x C Substrate' interaction (Supplementary Table S1). After 168 h, respired C from xylose (simple C) was significantly greater than from hemicellulose (more complex C). This relationship (xylose > hemicellulose) was consistent for all soils, despite significant differences in the overall amount of substrate C respired among soils (Fig. 2). There was no significant effect of nutrient treatment on substrate-respired C in any treatment combination or soil.

The direction and magnitude of primed C after 168 h varied among soils, C substrates and nutrient treatments, with significant 'Soil x C Substrate' and 'Soil x Nutrient' interactive effects (Supplementary Table S1). Soils from lower elevations (210 m and 1500 m) exhibited positive or negligible priming responses, dependent on the complexity of added C substrates (Fig. 3 c-d). By contrast, soils from higher elevations (3025 m and 3644 m) typically displayed negative priming responses (reduced mineralisation of SOM), the magnitude of which was dependent on nutrient treatments (Fig. 3 a-b).

For the upper montane forest (3025 m) and grassland (3644 m) soils, amendment with C substrates had a relatively minor influence on primed C, with no significant difference among responses to control (no added C), hemicellulose and xylose treatments (Fig. 3 a-b). Instead, for these soils, priming responses varied significantly among nutrient treatments, whereby priming induced by N and NP (both alone and in combination with C) was more negative compared to soils without added nutrients. There was no significant difference among responses to N and NP treatments for these soils. Amendment of the montane grassland soil with xylose +P enhanced the mineralisation of SOM (positive priming), compared to the negative priming induced by xylose alone (Fig. 3a), a response not evident in the upper montane forest soil.

In the lower montane forest (1500 m) and lowland forest (210 m) soils, the magnitude of priming responses after 168 h varied with C substrate, whereby xylose stimulated significantly greater priming of SOM compared to hemicellulose (Fig. 3 c-d). Greater priming of SOM following amendment with xylose was, however, likely a function of greater mineralisation of the more labile xylose substrate over the 7-day experimental period, rather than greater priming of SOM stimulated by xylose *per se*, as for these soils the proportion of primed to substrate-derived C did not differ depending on amendment with xylose or hemicellulose (Supplementary Fig. S1). Amendment of these lower elevation soils with labile nutrients had no significant effect on priming responses, with no significant differences among control, N, P and NP treatments (both when nutrients were added alone and in combination with C substrates).

3.3. Microbial assimilation of ^{13}C substrates and excess soil C

Total incorporation of C substrates in microbial PLFAs varied significantly among soils but not among C substrates or nutrient treatments (Supplementary Table S3). More substrate-C was incorporated into microbial PLFAs in the upper montane forest soil (3025 m) compared to the lowland forest soil (210 m; Fig. 4). The index of microbial substrate-CUE was also greater in the upper montane forest soil (Fig. 4). The complexity of added C substrates had a marginal effect (p = 0.06) on microbial substrate-CUE, whereby the CUE of hemicellulose was marginally greater compared to xylose in the lowland forest soil. In both upper montane and lowland forest soils, fungi assimilated a greater proportion of xylose compared to hemicellulose and GP bacteria assimilated a greater proportion of hemicellulose compared to xylose (Fig. 5). In the upper montane forest soil, GN bacteria assimilated a greater proportion of xylose compared to hemicellulose, whereas in the lowland forest soil assimilation of both C substrates by GN bacteria was low, with no significant difference in the relative proportion of xylose and hemicellulose assimilated (Fig. 5).

Nutrient treatments had no significant effect on the total incorporation of C substrates in microbial PLFAs, nor the relative proportion of substrate-C assimilated by different functional groups (Supplementary Table S3). However, nutrient treatments did influence microbial assimilation of excess soil-derived C in some cases (Fig. 6). In

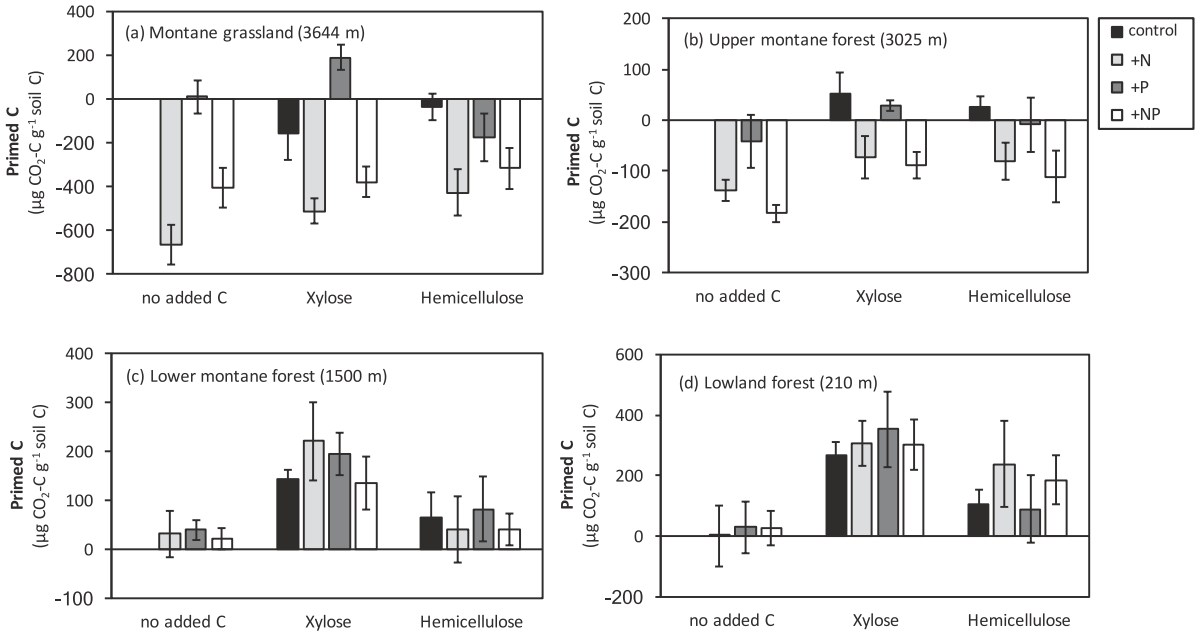

Fig. 3. Cumulative primed C (μg CO_2-C g^{-1} soil C) from (**a**) montane grassland, (**b**) upper montane forest, (**c**) lower montane forest and (**d**) lowland forest soils 168 h following amendment with C substrates (no added C, xylose and hemicellulose) in combination with nutrient treatments (control, +N, +P, +NP). Data represent mean ± 1SE (n = 4). Note different y-axis scales among panels a–d.

the upper montane forest soil, GP bacteria incorporated greater amounts of soil-derived C when amended with xylose alone, with incorporation of soil-derived C by all microbial functional groups reduced when xylose was added in combination with N (Fig. 6a). Microbial incorporation of soil-derived C was also reduced following amendment of upper montane soils with hemicellulose, but most strongly in response to hemicellulose alone, and to a lesser degree when hemicellulose was added in combination with N or P (Fig. 6b). In the case of the lowland forest soil, xylose typically had a negligible influence on the incorporation of soil-derived C in PLFAs (Fig. 6c), while amendment with hemicellulose marginally increased assimilation of soil-derived C in microbial PLFAs (Fig. 6d), with no clear differences in soil C incorporation dependent on added nutrient treatments.

4. Discussion

4.1. Microbial mineralisation of ^{13}C substrates and priming of SOM

Substrate respired CO_2-C was unaffected by nutrient additions for all of the soils (Fig. 2); a finding which was in broad contrast to other studies. While N addition has been shown to suppress the decomposition of lignin-rich plant material (Carreiro et al., 2000; Knorr et al., 2005), other studies have often found decomposition of plant material or added C substrates to be greater when inorganic nutrients were added, indicating nutrient constraints to decomposition. This includes patterns of increased decomposition with N addition in some temperate (Knorr et al., 2005; Manning et al., 2008; Vivanco and Austin, 2011) and tropical montane ecosystems (Hobbie, 2000), and with P addition in tropical lowland forests (Cleveland et al., 2002; Nottingham et al., 2012, 2015c; Chen et al., 2016). The differing outcome in our study indicates that the mineralisation of added C substrates was not limited by N or P. This lack of effect of N or P on the turnover of added substrates may reflect that substrate metabolism was constrained by the availability of other nutrients (e.g. potassium; Kaspari et al., 2008), or may be a consequence of the low soil pH across all our study sites (Table 2), which can lead to increased sorption of P to minerals (Olander and Vitousek, 2004). Consistent with this, it has been shown for a range of tropical forest soils that the greatest effect of nutrients in enhancing the turnover of added C substrates occurred when soil pH was neutral to mildly acidic (Nottingham et al., 2015c). Alternatively, it is possible that soil microorganisms in our study used the labile substrate-C in preference to more recalcitrant soil-C, without

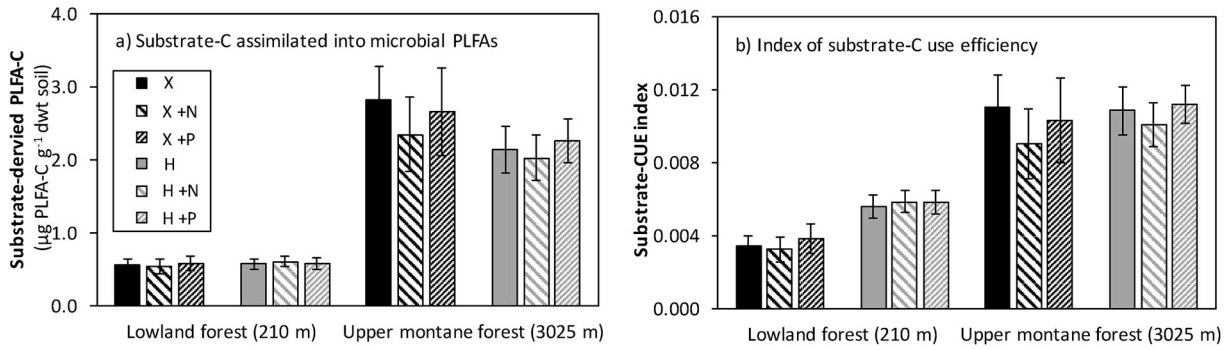

Fig. 4. (**a**) Assimilation of substrate-C into microbial PLFAs, and (**b**) an index of microbial substrate-carbon use efficiency (CUE) in lowland forest and upper montane forest soils, following amendment with C substrates (xylose; X and hemicellulose; H) in combination with nutrient treatments (control; no added nutrient treatment, +N, +P). Bars represent mean ± 1SE (n = 3).

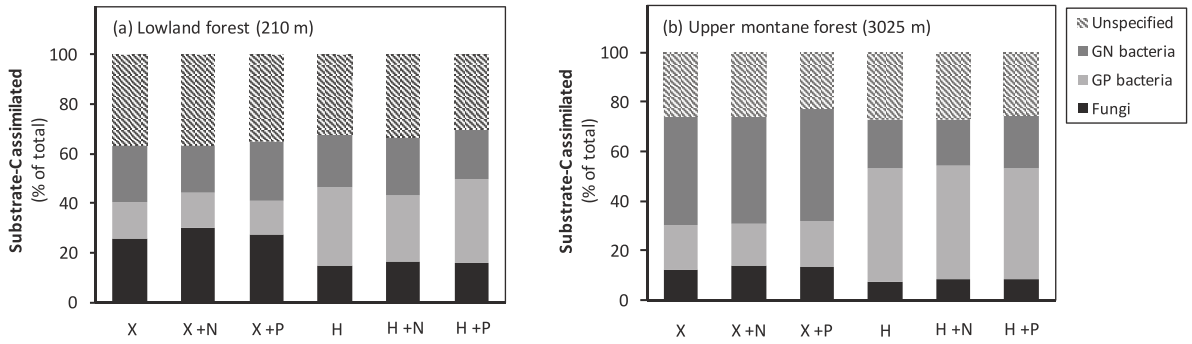

Fig. 5. Relative proportion (as % of total substrate incorporation into all PLFAs) of C substrate assimilated into PLFA biomarkers indicative of key microbial functional groups (fungi, gram positive bacteria; GP, gram negative bacteria; GN and unspecified PLFAs), following amendment of (**a**) lowland forest and (**b**) upper montane forest soils with xylose (X) and hemicellulose (H) in combination with nutrient treatments (control; no added nutrient, +N, +P). Data represent mean (n = 3).

nutrient constraint. Accordingly, even in the absence of added N or P, microorganisms may have been able to acquire sufficient nutrients from the soil to mineralise the relatively low concentration of added C, with nutrient availability instead influencing the mineralisation of native SOM in some cases (Fig. 3 a-b). This dichotomy of different nutrient constraints to added labile C and SOM-derived C has been shown elsewhere in tropical forest (Nottingham et al., 2015c) and temperate grassland soils (Carrillo et al., 2017).

Nitrogen addition had a large influence on SOM decomposition in upper montane forest and grassland soils. In these soils, amendment with C substrates alone had a relatively minor influence on priming of SOM, but addition of N (with or without P) significantly reduced the release of SOM-derived CO_2 (Fig. 3 a-b). Negative priming responses to N have also been widely reported elsewhere (Bird et al., 2011; Poeplau et al., 2016; Tian et al., 2016), with reduced mineralisation of SOM under elevated N availability attributed to preferential use of the exogenous N source (Craine et al., 2007; Dijkstra et al., 2013; Chen et al., 2014). Previous studies of this elevation gradient in Peru have identified high microbial demand for N at higher elevations, because N addition increased decomposition (Fisher et al., 2013), and the relative investment into N-degrading enzymes increased at higher elevations (Nottingham et al., 2015b). Our findings further suggest that the turnover of organic matter in these montane soils is regulated by microbial demand for N. In these soils, which are high in organic N but low in available $NH_4 + NO_3$ (Table 2; Nottingham et al., 2015b), there appears to be a high degree of baseline microbial N-mining from SOM, such that in the absence of external nutrients, microbial demand is met by mineralising SOM to acquire N. Consequently, the increased availability of inorganic N following the nutrient addition in our study may have alleviated microbial demand for N and therefore reduced microbial N-mining, resulting in reduced SOM mineralisation (negative priming).

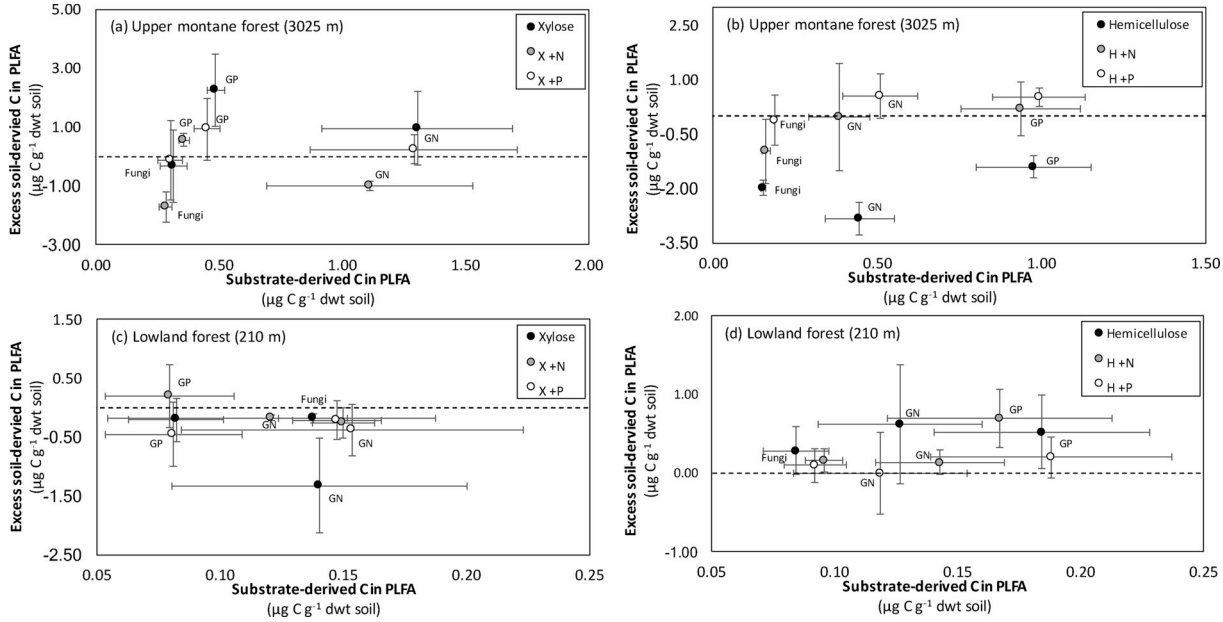

Fig. 6. Concentrations of substrate-derived C (µg substrate-C g^{-1} dwt soil) and excess soil-derived C (µg soil-C g^{-1} dwt soil) in microbial PLFAs (gram-positive bacteria; GP, gram-negative bacteria; GN, and fungi) following amendment with C substrates (xylose or hemicellulose) alone and in combination with +N or + P in (**a**) upper montane forest soil (xylose addition), (**b**) upper montane forest soil (hemicellulose addition), (**c**) lowland forest soil (xylose addition) and (**d**) lowland forest soil (hemicellulose addition). Microbial groups which appear above the dashed line (y = 0) exhibited increased incorporation of soil-derived C, whereas those which appear below the dashed line exhibited reduced incorporation of soil-derived C, relative to PLFAs in untreated control soils. Data represent mean ± 1SE (n = 3). Note differences among axis scales.

Carbon substrate addition in lower montane and lowland forest soils induced positive priming, which was greatest in response to xylose (Fig. 3 c-d). Consistent with this, inputs of labile C were previously found to induce positive priming in tropical lowland soils from Peru (Whitaker et al., 2014a) and Panama (Nottingham et al., 2012, 2015c). Amendment of lowland soils with C substrates in combination with P and/or N in our study, however, had no significant additional influence (Fig. 3 c-d). This suggests that priming of SOM in these soils was not determined by microbial demand for P (or N), despite the very low availability of inorganic P in the lowland forest soil (Table 2). The lack of a nutrient effect in reducing priming in lowland soils could be due to rapid immobilisation (high sorption) of added nutrients in low pH soils, limiting their availability to microbes (Olander and Vitousek, 2004), with low pH potentially also affecting related enzyme function (Frankenberger and Johanson, 1982; Sinsabaugh et al., 2008) and microbial community composition (Rousk et al., 2010). The lack of a P effect on priming in particular may reflect the numerous pathways for microbial P acquisition which do not destabilise C (Dijkstra et al., 2013), including P mineralisation by biochemical hydrolysis (McGill and Cole, 1981), and P acquisition from inorganic sources (Walker and Syers, 1976). Although there is evidence that priming due to coupled acquisition of C and P can occur (Nottingham et al., 2012; Spohn et al., 2013; Meyer et al., 2018), it may be less common given the opportunities for P acquisition from other sources. For example, in 11 lowland tropical forest soils where C-metabolism was predominantly P-limited, N rather than P was the predominant constraint on priming of SOM (Nottingham et al., 2015c). Similarly, there was no relationship between P availability and priming responses across a substrate-age gradient in tropical forest (Sullivan and Hart, 2013). In our study, therefore, the positive priming responses in lower montane and lowland forest soils following C amendment may have occurred due to a constraint other than N or P, or by a mechanism other than nutrient mining (e.g. due to stimulation of specific groups of recalcitrant C degrading microorganisms; Fontaine et al., 2003; Pascault et al., 2013; Su et al., 2017).

The direction of priming responses to C-amendment observed in our study were generally consistent with those identified previously for the same Peruvian gradient (Whitaker et al., 2014a). However, previously, the nitrogenous C-substrate glycine elicited strong positive priming effects in both lowland and montane forest soils. By contrast, addition of C substrates in combination with N (as NH_4-NO_3) here reduced mineralisation of pre-existing SOM in higher elevation soils (Fig. 3 a-b) and had no effect in soils from lower elevations (Fig. 3 c-d). These differences may be attributed to the different sources by which C and N were supplied. Amendment of soils with trace amounts of amino acids such as glycine has been shown to trigger activation of soil microorganisms (De Nobili et al., 2001; Mondini et al., 2006) and, as such, glycine may have stimulated microbial metabolism, resulting in strong priming of SOM (Mason-Jones and Kuzyakov, 2017). Whereas here, microorganisms in the higher-elevation soils appeared to use the exogenous supply of N *instead* of mineralising SOM to acquire N (resulting in negative priming). Differences in the stoichiometry of C and N inputs may have also influenced the direction of priming responses (Qiao et al., 2016). Thus, the direction of priming may be sensitive to the chemical composition or stoichiometry of N inputs, which merits further investigation.

4.2. Microbial assimilation of ^{13}C substrates and excess soil-derived C

Nutrient treatments had no significant influence on microbial incorporation of C substrates, however the complexity of C substrates was an important determinant of assimilation by different microbial groups (Fig. 5). Gram-negative bacteria are most often associated with the mineralisation of labile C, while gram-positive bacteria are thought to target more complex C sources (Fierer et al., 2007; Kramer and Gleixner, 2008), in broad agreement with our findings (Fig. 5). Although fungi are often associated with the degradation of more complex C-compounds (Cusack et al., 2011a; Müller et al., 2017), some fungal taxa have been shown to use more labile C sources (Hanson et al., 2008; Lemanski and Scheu, 2014). This was evident here, where fungi assimilated a greater proportion of the simple C substrate, particularly in the lowland forest soil (Fig. 5). Our results demonstrate that C use within the microbial communities under study is more strongly shaped by the chemical complexity of organic matter and the functional capacity of microbial taxa, rather than the availability of nutrients. Nutrient availability may instead play a role in shaping the composition of the microbial community, as some studies have reported microbial community shifts in response to long-term fertilisation (Güsewell and Gessner, 2009; Liu et al., 2013; Fanin et al., 2015a). While there was no change in microbial composition 7 days after nutrient treatments were added (Supplementary Fig. S2), the duration of our study may have been too short to observe a response. Alternatively, the nutrient treatments may have been too small relative to the inherent nutrient status of the soil to drive a compositional change, as a recent meta-analysis of N addition studies revealed stronger microbial responses to fertilisation with increasing study duration and nutrient addition-rates (Zhou et al., 2017).

In the upper montane forest soil, assimilation of soil-derived C by GP bacteria increased following amendment with xylose, while assimilation of soil-derived C by all microbial groups was reduced when xylose was added in combination with N (Fig. 6a). These findings are consistent with the priming responses identified from the change in CO_2 production (Fig. 3b), further supporting reduced mining of N from SOM when N was externally supplied. Some studies have associated fungi with N-mining (Fontaine et al., 2011; Rousk et al., 2016; Soares et al., 2017), while in another study, *K*-strategists (i.e. microorganisms associated with a slow but more efficient growth strategy) were identified as responsible for priming of SOM to acquire N (Chen et al., 2014). Although the microbial functional divisions used here do not directly correspond to the spectrum of *r-K* growth strategies, GP bacteria and fungi are often recognised as *K*-strategists, with slow growth rates and capacity to use more recalcitrant C-sources (Fierer et al., 2007; Dungait et al., 2013). Results from our study also suggest that, when supplied with labile C, GP bacteria increased mineralisation of SOM, to mine N. Incorporation of excess soil-derived C by fungi in response to xylose alone was, however, negligible, suggesting that fungi were not associated with positive priming of SOM for N-acquisition in these soils.

In the lowland forest soil, amendment with hemicellulose tended to increase assimilation of soil-derived C in microbial PLFAs, particularly into GP bacteria (Fig. 6d), consistent with the small positive priming response identified from CO_2 production (Fig. 3d). Amendment of these lowland soils with xylose, however, had a negligible influence on excess soil-derived C assimilation by all microbial groups (Fig. 6c). This may seem surprising, given the magnitude of positive priming induced by the xylose treatment (Fig. 3d). However, the index of microbial substrate-CUE determined for these lowland forest soils was low (Fig. 4b), favouring respiration of mineralised substrate-C rather than assimilation into microbial PLFAs (Manzoni et al., 2012). Given this, it may be expected that primed soil-C mineralised by these microorganisms would be mostly respired or invested in the synthesis of extracellular enzymes, with a very low proportion incorporated into PLFAs for growth, perhaps explaining why no increase in soil-C assimilation was detected here.

4.3. Conclusion

The mineralisation of simple and more complex C substrates was not affected by nutrient availability in contrasting fertility soils from a 3400 m tropical elevation gradient. However, the direction and intensity of priming responses varied among soils and was in some cases dependent on the availability of N. Strong negative priming responses in upper montane forest and grassland soils to exogenously supplied N

suggest that turnover of SOM in these soils was regulated by microbial demand for N, resulting in reduced mineralisation of SOM when N was externally supplied. Whereas, microbial activity in lower montane and lowland forest soils was not influenced by N or P additions. While inferences based upon short-term laboratory experiments must be drawn with caution, evidence from long-term experimental studies elsewhere suggest that both positive and negative priming responses to altered C and nutrient supply can persist with time (Martikainen et al., 1989; Sayer et al., 2011). Long-term N fertilisation of tropical montane forests in Puerto Rico (Cusack et al., 2011b), and a young subtropical forest in China (Fan et al., 2014), has been shown to increase soil C stocks. As such, our findings may provide a potential mechanism for this response, whereby inputs of N could constrain the turnover of SOM, due to reduced mining of SOM for N acquisition. Given that N deposition is projected to increase rapidly in the tropics over the coming decades (Galloway et al., 2004), reduced N-mining could have a positive effect on soil C sequestration in high elevation montane systems. By contrast, changes to nutrient supply in tropical lowland forest soils may not influence the turnover of SOM. Instead, increased inputs of labile plant-derived C, for example as a consequence of elevated atmospheric CO_2 (Cusack et al., 2016), may stimulate positive priming and induce C loss from lower elevation tropical soils.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.soilbio.2018.10.015.

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