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RESEARCH ARTICLE

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Nutrient limitation or home field advantage: Does microbial community adaptation overcome nutrient limitation of litter decomposition in a tropical peatland?

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Abstract

1. Litter decomposition is an important control on carbon accumulation in tropical peatlands. Stoichiometric theory suggests that decomposition is regulated by elemental ratios in litter while the home field advantage (HFA) hypothesis predicts that decomposer communities are adapted to local conditions. To date, the relative importance of these contrasting theories for litter decomposition and therefore the carbon balance of tropical peatlands remain poorly understood.
2. We conducted two in situ litter decomposition experiments in a lowland tropical peatland. The first experiment tested the importance of the stoichiometric theory using a factorial nutrient addition experiment at two sites with contrasting vegetation (*Raphia taedigera* and *Campnosperma panamensis*) to assess how nutrient addition affected microbial enzyme activity and litter mass loss at the peat surface and at 50 cm depth. The second experiment tested the importance of HFA by reciprocal translocation of leaf litter from *R. taedigera* and *C. panamensis* forests, which differed in both litter chemistry and soil nutrient availability, to separate the influence of litter chemistry and soil/site properties on litter mass loss.
3. The activities of hydrolytic enzymes involved in the decomposition of large plant polymers were stimulated by nitrogen addition only where nitrogen availability was low relative to phosphorus, and were stimulated by phosphorus addition where phosphorus availability was low.
4. The addition of nitrogen, but not phosphorus, increased leaf litter decomposition under waterlogged conditions at 50 cm depth, but not at the peat surface.
5. Decomposition was greatest for autochthonous litter irrespective of site nutrient status, indicating that adaptation of the microbial community to low nutrients can partly overcome nutrient limitation, and suggesting that HFA can influence litter decomposition rates.
6. *Synthesis.* Our study shows that leaf litter decomposition and the activity of microbial enzymes in tropical peatlands are constrained in part by nutrient availability. However, such nutrient limitation of litter decomposition can be overcome by adaptation of the microbial community.

KEYWORDS
carbon turnover, nitrogen, nutrient dynamics, phosphorus, tropical peat

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1 | INTRODUCTION

Decomposition rates of organic matter influence carbon storage and regulate nutrient availability in natural ecosystems. Decomposition is carried out by complex groups of micro-organisms and the rate of decomposition is controlled by how the substrate properties, together with the abiotic environment, meet the demands of the microbial communities (Kaiser, Franklin, Dieckmann, & Richter, 2014). According to stoichiometric theory, the balance of carbon (C), nitrogen (N) and phosphorus (P) that decomposer organisms must maintain to regulate metabolic function and growth limits decomposition rates when nutrient ratios in the substrate do not match demand by individual micro-organisms (Manzoni & Porporato, 2009; Sterner & Elser, 2002). If this holds true, decomposition rates should not be limited by nutrient availability when the composition (with regards to C, N and P) of the substrate (e.g. leaf litter) is similar to that of the decomposer organisms. Indeed, greater nutrient availability enhances decomposition in a wide range of ecosystems (e.g. subarctic heaths, mangroves), supporting the notion of nutrient limitation of decomposition (Cornwell et al., 2008; Keuskamp, Hefting, Dingemans, Verhoeven, & Feller, 2015; Quested, Callaghan, Cornelissen, & Press, 2005). However, in other instances nutrient addition has had limited effects on decomposition rates (e.g. decomposition of low quality litter has been found to be energy rather than nutrient-limited; Keuskamp, Schmitt, Laanbroek, Verhoeven, & Hefting, 2013; Knorr, Frey, Curtis, & Knorr, 2005). Furthermore, nutrient limitation of litter decomposition fluctuates over time, reflecting changing nutrient demands of the decomposer organisms as well as changes in litter chemistry as decomposition progresses (Kaiser et al., 2014).

Micro-organisms can overcome resource limitation by up-regulating the production of extracellular enzymes involved in C, N and P acquisition, depending on which nutrients are limiting their growth (Sinsabaugh & Follstad Shah, 2012). For example, low P availability increases the activity of acid phosphatases in a range of soils (Allison, Condron, Peltzer, Richardson, & Turner, 2007; Olander & Vitousek, 2000; Sjögersten, Cheesman, Lopez, & Turner, 2011), while low nutrient availability can drive tight nutrient cycling within microbial communities (Kaiser et al., 2014). Strong interactions between the composition and functioning of the microbial community and the dominant litter inputs are one of the explanations of the so called "home field advantage" (HFA), whereby the decomposer community becomes adapted, or optimized, to degrade the litter at a given site (Austin, Vivanco, González-Arzac, & Pérez, 2014). This results in faster litter decomposition rates when litter decomposes adjacent to the plants that produced it (Vivanco & Austin, 2008). This pattern is relatively weak, but holds true at the global scale, with an *c*. 8% greater mass loss when litter material was decomposing at "home" (Ayres et al., 2009; Veen, Freschet, Ordonez, & Wardle, 2015). However, the effects of the HFA are more pronounced when sites differ considerably in soil nutrient availability and plant species composition, suggesting lower degree of redundancy among decomposer communities across locations with strongly contrasting soil and litter type characteristics (Veen et al., 2015).

Lowland tropical peatlands have the fastest rates of peat accumulation in the world—up to 10 times faster than temperate, subarctic and boreal peatlands (Chimner & Ewel, 2005; Dommain, Couwenberg, & Joosten, 2011; Gorham, Janssens, & Glaser, 2003)—and contain 40–90 Gt of C (Kurnianto et al., 2015). The functioning of tropical peatlands as a C store is currently under threat as land-use change, climate change and increasing levels of atmospheric N deposition accelerate decomposition rates (Bragazza et al., 2012; Galloway et al., 2004; IPCC, 2013). If nutrient availability is a key limitation of decomposition in tropical peatlands, as has been found at higher latitudes (Wang, Moore, Talbot, & Richard, 2014), then greater nutrient availability might reduce C storage. In addition, nutrient availability shapes the species composition of peat swamp forests (Brady, 1997; Page, Rieley, Shotyk, & Weiss, 1999; Sjögersten et al., 2011; Troxler, 2007) and hence the quality and the quantity of litter inputs (Hoyos-Santillan et al., 2016; Wright, Black, Cheesman, Turner, & Sjögersten, 2013), with implications for the composition of the decomposer community (Troxler et al., 2012) and decomposition rates (Hoyos-Santillan et al., 2015; Yule & Gomez, 2009).

Litter decomposition of tropical peatland tree species varies among species (e.g. between palms and hardwoods) and tissue types (e.g. between roots and leaves; Hoyos-Santillan et al., 2015; Yule & Gomez, 2009). Furthermore, the degree of waterlogging and nutrient availability, as well as microbial community composition, pH, and concentrations of dissolved oxygen and phenolic compounds, vary within peat profiles (Freeman, Ostle, & Kang, 2001; Hoyos-Santillan et al., 2015, 2016; Jackson, Liew, & Yule, 2009). Therefore, decomposition rates of the same litter material differ depending on its position within the peat profile (Hoyos-Santillan et al., 2015).

To test the importance of stoichiometric theory (Manzoni & Porporato, 2009; Sterner & Elser, 2002) and HFA (Austin et al., 2014) for litter decomposition, we carried out two experiments in a tropical peatland in Panama. The first experiment was a factorial N and P addition experiment in two contrasting forest types, a nutrient-rich palm swamp and a relatively less nutrient-rich mixed forest (Sjögersten et al., 2011). This experiment tested the hypothesis that nutrient availability controls (1) activities of extra cellular hydrolytic enzymes, which are involved in microbial nutrient and carbon acquisition and (2) litter decomposition. The experiment involved decomposing different litter tissue types (leaves, roots and stems) at the peat surface and at 50 cm depth. We predicted that if the microbial community at a site was nutrient-limited, nutrient addition would reduce microbial C:N and C:P ratios and down-regulate enzymes involved in nutrient acquisition, resulting in a subsequent up-regulation on enzymes involved in the breakdown of sugars, hemi-cellulose and cellulose (Sinsabaugh & Follstad Shah, 2012). According to stoichiometric theory, we expected nutrient addition to accelerate litter mass loss at the low nutrient mixed forest site, and that litter decomposition would

be greatest for both litter types at the more nutrient-rich palm swamp site. We also predicted that litter with high C:N and C:P ratios would be more responsive to nutrient addition with respect to mass loss, in agreement with Baumann, Marschner, Smernik, and Baldock (2009).

The second experiment was a reciprocal leaf litter translocation experiment between the two contrasting forest types. This experiment tested the hypothesis that litter is decomposed faster at "home" than "away" irrespective of site nutrient status (Austin et al., 2014; Kaiser et al., 2014). For this experiment, we carried out reciprocal transplants of leaf litter material from two different trees species that were the dominant trees at two peatlands sites with contrasting nutrient status (i.e. the same two sites that were used for the nutrient addition experiment). We predicted that according to the HFA theory, the "home" palm leaf litter would degrade more rapidly at the palm site while the litter from the low nutrient mixed forest would degrade fastest at the mixed forest site, i.e. its home location (Veen et al., 2015). This contrasts with our prediction above of greater decomposition at the nutrient-rich site following stoichiometric theory (e.g. Sterner & Elser, 2002), allowing us to investigate the respective influences of HFA and stoichiometric theory on C dynamics and, by extension, peat accumulation in tropical peatlands.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted in the north-west Caribbean coast of Panama where several large peatlands are located within the Bocas del Toro province (Phillips, Rouse, & Bustin, 1997). Rainfall averages 3092 ± 181 mm/year, with a mean annual air temperature of 25.9 ± 0.3°C (2003–2011; Smithsonian Tropical Research Institute Physical Monitoring Program). There is no pronounced seasonality (Wright et al., 2011), although there are two periods of reduced rainfall from February to April and August to September.

Seven phasic communities have been identified in these peatlands (Phillips et al., 1997). We studied two of these: palm swamp dominated by *Raphia taedigera* (Mart.), a canopy forming palm in the Arecaceae family (9°25′29.20″N, 82°24′05.60″W), and mixed forest dominated by *Campnosperma panamensis* (Standl), an evergreen broadleaved hardwood tree in the Anacardiaceae family (9°25′15.00″N, 82°24′14.64″W). The sites were located within the Changuinola peat deposit in the San San Pond Sak wetland (Ramsar site No. 611; ≈164 km^2). The distance between the sites was *c*. 300 m. Both sites are freshwater (surface water conductivity <200 μS/cm), with the water-table predominantly at or just below (10 cm) the peat surface. Maximum recorded water fluctuations were +15 to −40 cm relative to the peat surface, with surface water consistently above the peat surface during periods of high rainfall. Dissolved O_2 concentrations in the pore water were up to 3.3 ppm at the surface (Palm swamp: 1.35 ± 0.25 ppm; Mixed forest: 2.15 ± 0.34), but as low as 0.2 ppm at 50 cm below-ground (Palm swamp: 0.72 ± 0.27 ppm; Mixed forest: 0.68 ± 0.19). Nutrient levels at the two sites differ with respect to total and exchangeable P (higher at the palm swamp), as well as microbial N and P (higher at the palm site) and peat C:N and C:P ratios (higher at the palm swamp site; Sjögersten et al., 2011). Palm sites had large amounts of palm leaf litter at the surface and a dense but shallow (1.1 m depth) fibrous root system (Wright et al., 2011). The mixed forest sites had large amounts of *C. panamensis* leaf litter at the surface but leaf litter from other species was also present (for further details on of the forest structure and composition see Hoyos-Santillan et al., 2016; Sjögersten et al., 2011). *Campnosperma panamensis* is characterized by woody lignified structural roots reaching at least 1 m depth and abundant surface knee roots (Wright et al., 2011). Microtopography within all sites consisted of shallow ponds and raised areas (close to trees associated with root structures).

2.2 | Experimental design and methodology

2.2.1 | Nutrient addition experiment

The potential role of nutrient limitation on microbial activity and litter decomposition was explored by a 5-month (October 2011 to March 2012) litterbag experiment. The nutrient treatments were: N, P, N+P and control (Ctrl). The experiment consisted of ten blocks distributed along 150 m transects running from south-east to north-west at both the palm swamp and mixed forest sites (20 blocks in total). Each block was 10 × 10 m with the nutrient enrichment treatments applied at each corner, blocks were 5 m apart (Figure 1). Adjacent corners had the same nutrient treatment.

Raphia taedigera and *C. panamensis* litter for the decomposition study was collected from the palm swamp and mixed forest, respectively. The collected litter consisted of recently senesced leaves, freshly cut leaf stalks (petioles) or stems (*c*. 5 cm in diameter), and fine lateral roots (2–4 mm diameter) from the top 20 cm of the soil profile. After collection, the litter was cleaned with deionized water and air dried for 5 days. To allow comparable masses to be weighed out, the litter material was cut into smaller pieces: leaves were cut into *c*. 2 × 2 cm pieces, roots were cut into *c*. 2 cm lengths, and stems were cut into *c*. 1 cm thick discs to ensure that a cross-section of the stem tissue was used. Litter was weighed (leaves: *c*. 2 g; whereas stems and roots: *c*. 1 g), placed separately into pre-weighed polyester mesh litterbags (10 × 10 cm; 560 μm mesh), and tied with polyamide thread (⌀ = 0.8 mm). Litterbags were placed directly on the peat surface avoiding hollows. For the below-ground incubation (50 cm depth), a narrow slit was cut into the peat and litterbags were manually pushed to the right depth. To aid recovery, litterbags were tied to a string which was securely attached to the ground surface. One litterbag of each tissue type was placed at each of the incubation locations at the start of the experiment, giving a total of 480 litterbags (2 depths (surface and 50 cm depth) × 3 tissue types (leaves, stems, roots) × 4 nutrient treatments (Ctrl, N, P and N+P) × 2 sites (palm swamp and mixed forest) × 10 blocks).

Nutrient enrichment was applied once at the beginning of the experiment by filling 25 cm sections of dialysis tubing (Spectra/Por®

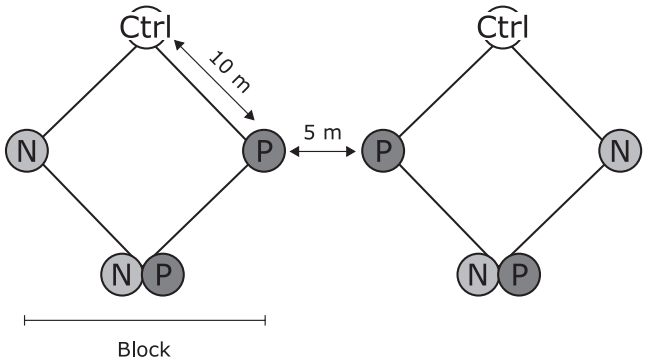

FIGURE 1 Schematic diagram outlining the experimental set up for the nutrient addition, (Ctrl) control, (N) nitrogen and (P) phosphorous. The same set up was used at the palm swamp and the mixed forest sites. Ten blocks were set up at each site with litterbags placed both at the peat surface and at 50 cm depth

membrane: 40 mm diameter, 6,000–8,000 molecular weight cut off) with 0.86 mol of either N (Urea: $CO(NH_2)_2$ or P (calcium phosphate monobasic monohydrate: $Ca(H_2PO_4)_2{\cdot}H_2O$) fertilizer. This allowed a slow release of nutrients through the membrane (Feller, 1995). Within each block, fertilizer was applied at both the surface and below-ground (50 cm) adjacent to the litterbags (<10 cm from litterbags). For the below-ground treatment, the dialysis tubes were inserted in a narrow vertical slit cut into the peat.

After 5 months, soil samples were collected to evaluate the impact of the nutrient treatments on surface peat properties (i.e. extractable and microbial nutrients, and hydrolytic enzyme activities). To do this, 10 × 10 × 10 cm samples of peat were carefully cut from the surface peat where the litterbags were incubated. Soil samples were stored in plastic bags at 4°C for 1 week prior to nutrient and enzymatic analyses.

The increase of available nutrients after the nutrient addition treatment, dissolved organic C (DOC) and dissolved N fractions (TDN = dissolved organic nitrogen + inorganic fraction (nitrate-nitrite and ammonium)) were extracted from surface peat (10 cm depth) by shaking 40 g (fresh weight) of peat in 75 ml of 0.5 M K_2SO_4 for 1 hr (Sjögersten et al., 2011). Extracts were centrifuged (8,000 *g*, 15 min) and DOC and TDN in the supernatant were determined after a five-fold dilution by TOC-TN analyser (Shimadzu, Columbia, MD, USA). Readily exchangeable P was determined by extraction with anion-exchange membranes (Myers, Thien, & Pierzynski, 1999; Turner & Romero, 2009). For this purpose, surface peat (20 g fresh weight) was shaken for 24 hr with 80 ml deionized water and five anion-exchange resin strips (1 × 40 mm; manufactured by BDH Prolabo). The strips were rinsed in deionized water and the phosphate recovered by shaking for 1 hr in 50 ml of 0.25 M H_2SO_4. Phosphate was determined in the acid solution at 880 nm following online neutralization and automated molybdate colorimetry using a flow injection analyser (Lachat Quikchem 8500; Hach Ltd, Loveland, CO, USA).

To investigate the relationship between the nutrient treatments and microbial activity, we measured, in the peat, microbial biomass C, N and P, and extracellular hydrolytic enzyme activities; these parameters were used as indicators of the functioning of the microbial community at the two experimental sites. Microbial C and N were estimated by $CHCl_3$ fumigation and 0.5 M K_2SO_4 extraction using a correction factor of 2.64 to account for the unrecovered biomass C (Vance, Brookes, & Jenkinson, 1987) and 1.85 to account for unrecovered biomass N (Brookes, Landman, Pruden, & Jenkinson, 1985). Microbial P was determined by extraction by hexanol fumigation and anion-exchange membranes as described previously (Myers et al., 1999; Turner & Romero, 2009). Microbial P was calculated as the difference between phosphate in fumigated and unfumigated samples.

Total C and N were measured in initial litter and peat samples collected from the peat surface and 50 cm depth. Litter and peat samples were ball milled prior to analysis on a total element analyser (Thermo Flash EA 1112; CE Instruments, Wigan, UK). Peat and litter ash from loss-on-ignition analysis was dissolved in 6 M HNO_3 to estimate P concentration by molybdate colorimetry (Andersen, 1976). For detailed methods, see Hoyos-Santillan (2014).

To assess if nutrient addition altered the activity of enzymes involved in the release of C, N, P and sulphur from organic compounds, the activities of five different extracellular hydrolytic enzymes were measured at the end of the experiment using fresh surface peat collected from three of the nutrient addition experimental blocks at the palm swamp and the mixed forest. Assays were conducted using methylumbelliferone-linked fluorogenic substrates (Turner, 2010; Turner & Romero, 2009). Specifically, enzymes and substrates were: (1) phosphomonoesterase: 4-methylumbelliferyl phosphate; (2) phosphodiesterase: bis-(4-methylumbelliferyl) phosphate; (3) arylsulphatase: 4-methylumbelliferyl sulphate; (4) β-glucosidase: 4-methylumbelliferyl β-D-glucopyranoside; (5) *N*-acetyl-β-glucosaminidase: 4-methylumbelliferyl *N*-acetyl-β-D-glucosaminide. For the assays, peat (2 g fresh weight) was added to 200 ml of 1 mM sodium azide (NaN_3) solution and stirred for 10 min. Aliquots (50 μl) of peat suspension were dispensed into a 96-well microplate containing 100 μl of 200 μM substrate and 50 μl of sodium acetate-acetic acid buffer adjusted to pH 4 (the mean peat pH). Microplates were incubated at 30°C for 30 min; following incubation 50 μl of 0.5 M NaOH was added to terminate the reaction, and fluorescence was determined immediately on a FLUOstar Optima spectrofluorometer (BMG Labtech, Offenburg, Germany).

2.2.2 | Litter translocation experiment

The reciprocal litter translocation experiment involved incubating *R. taedigera* leaf litter in both a palm swamp and a mixed forest and vice versa for *C. panamensis*. The litter translocation used five of the ten blocks at the palm swamp and mixed forest; litterbags with leaves were installed at surface of the control corners of the odd numbered blocks. Total number of litterbags was 20 (i.e. 2 species × 2 sites × 5 replicates). The incubation time was 5 months and litter mass loss was quantified as in Section 2.2.3.

2.2.3 | Litterbag recovery

After collection, the litterbags were carefully rinsed with deionized water. It is possible that fine litter (<560 μm) was lost during the cleaning process, resulting in a slight overestimation of the mass loss during the incubation. After rinsing, bags were opened and the litter visually inspected to remove new root growth. Litter was then dried at 70°C for a minimum of 48 hr to constant weight in pre-weighted aluminium trays. The remaining mass of litter was calculated as a proportion of the initial mass remaining at the end of the experiment (Wieder & Lang, 1982).

2.3 | Statistical analyses

We used linear mixed models to assess the impact of the nutrient treatments on the measured parameters. The models were fitted using residual maximum likelihood (REML). To analyse the effect of the nutrients addition experiment on nutrient concentrations, ratios (C:N, C:P and N:P), hydrolytic enzyme activity, phasic community and nutrient treatment (Ctrl, N, P and N+P) were used as fixed factors and block as random factor. To analyse the effect of the nutrient addition on % litter remaining, the nutrient treatment (Ctrl, N, P and N+P), the different tissues, and the incubation depth were used as fixed factors, and block as random factor. The relationships between nutrient ratios in the extractable and microbial fractions were analysed using linear regression. For the analysis of the litter translocation experiment (% remaining $mass_{dw}$), the sites (palm swamp and mixed forest), and the translocation treatment were used as fixed factors, and block was the random factor. Residual plots were checked to ensure the assumption of normality and homogeneity of the residuals were met. We calculated the HFA index (HFAI), which quantifies the extent to which decomposition is faster or slower at home. Results throughout the text and figures are presented as *M* ± *SE*. Statistical analyses were performed in GenStat (VSN International, 2011).

2.3.1 | HFAI calculation

The HFAI is useful to evaluate the results obtained from the reciprocal experiment in the context of the HFA theory. The calculation was done according to Ayres et al. (2009). In order to do so, we calculated A_{RMLa}, A_{RMLb}, B_{RMLa} and B_{RMLb}; which represent the relative mass loss (RML) of leaves from one specie at a certain site. For instance, A_{RMLa} represents the RML of leaves from specie A at site a:

$$A_{RMLa} = \frac{A_a}{A_a + B_a} \times 100$$

where A_a and B_a correspond to the percent mass loss of leaf litter of two different species (i.e. A and B) at site a. From these, HFAI was calculated as follows:

$$HFAI = \left[\frac{A_{RMLa} + B_{RMLb}}{2} / \frac{A_{RMLb} + B_{RMLa}}{2} \right] \times 100 - 100$$

3 | RESULTS

3.1 | Differences in site and litter nutrient status

The two study sites differed in their nutrient status with greater TDN and readily exchangeable P concentrations at the palm swamp site, in line with Sjögersten et al. (2011). This difference was reflected in the nutrient status of the microbial community, which differed between the two sites: the palm swamp had higher microbial N and P concentrations, lower microbial C:N ratios, and higher microbial C:P ratios.

In control plots, C:N ratios were higher in the microbial fraction than in the extractable fraction, while C:P and N:P ratios were lower in the microbial fraction (Table 1). Freshly fallen litter had high C:N ratios but varied considerably among tissues and species with *R. taedigera* stems having the highest C:N ratio, and *R. taedigera* leaves having the lowest C:N ratio. *Raphia taedigera* litter C:P ratios were comparable to the surface peat, while the peat C:P ratios at 50 cm depth were much higher. The *C. panamensis* litter had a more variable C:P ratio than *R. taedigera* with leaf litter having four times as high ratios as root and stem tissue. The C:P ratios for all litter types for both species were considerably greater than in the peat extractable and microbial fractions. Litter N:P ratios were less than half of those found for surface peat, but higher than the N:P ratios in the microbial and extractable fractions.

3.2 | Nutrient addition experiment

3.2.1 | Extractable and microbial nutrients

Five months after the nutrient addition, TDN and readily exchangeable P were significantly greater in plots where nutrients were applied (N_{add}: $F_{1,28} = 8.71$, $p < .01$; P_{add}: $F_{1,56} = 7.67$, $p < .01$; Figure 2), apart from TDN concentrations at the palm site. Neither DOC nor microbial C varied significantly with nutrient addition (N_{add}: $F_{1,30} = 1.53$; $p > .05$; P_{add}: $F_{1,30} = 0.02$; $p > .05$). Microbial biomass N and P did not increase in response to the fertilization treatment (N_{add}: $F_{3,6} = 0.87$; $p > .05$; $F_{3,6} = 1.16$; $p > .05$; at the palm and mixed forest, respectively; P_{add}: $F_{2,11} = 1.04$; $p > .05$; $F_{2,10} = 1.71$; $p > .05$; at the palm and mixed forest, respectively; Figure 2). However, both the DOC/TDN (i.e. the extractable fraction; Site × N_{add}: $F_{1,12} = 13.66$; $p < .001$) and microbial C:N (Site × N_{add}: $F_{1,12} = 5.59$; $p < .05$) ratios decreased significantly in response to N addition at the low nutrient mixed forest site (Figure 3a,b); and there was a positive relationship ($F_{1,23} = 30.09$; $p < .001$; $R^2 = .56$) between the DOC/TDN and microbial C:N ratios (Figure 3c).

3.2.2 | Impacts of nutrient addition on extracellular enzymatic activity

Phosphomonoesterase activity was higher in the mixed forest site than at the palm swamp site ($F_{1,4} = 58.28$, $p < .01$) but was

TABLE 1 Mass-based ratios among C, N and P in different substrate types at the palm swamp and mixed forest sites

	Palm swamp			Mixed forest		
Ratio	C:N	C:P	N:P	C:N	C:P	N:P
Microbial	7.43 ± 0.16	5.29 ± 0.47	0.71 ± 0.07	8.25 ± 0.28	3.49 ± 0.47	0.43 ± 0.07
Extractable	3.87 ± 0.38	8.21 ± 1.11	2.13 ± 0.21	3.80 ± 0.44	28.76 ± 6.93	7.80 ± 2.29
Leaf[a]	37.71 ± na	911.5 ± na	24.17 ± na	127.9 ± na	3,984 ± na	31.16 ± na
Root[a]	55.91 ± na	1,155 ± na	20.65 ± na	78.19 ± na	1,034 ± na	13.22 ± na
Stem[a]	140.2 ± na	1,082 ± na	7.71 ± na	117.8 ± na	963.0 ± na	8.18 ± na
Peat (surface)[b]	41.53 ± na	1,142 ± na	45.24 ± na	35.13 ± na	1,274 ± na	98.78 ± na
Peat (−50 cm)[b]	19.79 ± na	5,642 ± na	196.9 ± na	40.73 ± na	3,001 ± na	76.27 ± na

[a]Litter are *Raphia taedigera* and *Campnosperma panamensis* for the palm swamp and mixed forest, respectively.
[b]Peat samples were taken before the nutrient treatment was applied (October 2011) from the top 10 cm of the peat profile.

not affected by nutrient addition ($F_{3,12}$ = 1.95, p > .05; Figure 4a). The activity of phosphodiesterase did not vary between sites ($F_{1,4}$ = 4.23, p > .05) or treatments ($F_{3,12}$ = 1.9, p > .05; Figure 4b). Arylsulphatase activity decreased with P addition ($F_{1,12}$ = 5.72, p < .05), while N addition increased arylsulphatase activity at the palm swamp but not at the mixed forest site (Site × N_{add}: $F_{1,12}$ = 5.5, p < .05; Figure 4c). β-glucosidase activity did not vary between sites (Figure 4d), but was increased by N addition at the palm swamp but not at the mixed forest (Site × N_{add}: $F_{1,12}$ = 4.03, p < .05). In contrast, P addition increased *N*-acetyl-β-glucosaminidase activity at the mixed forest but not at the palm swamp (Site × P_{add}: $F_{1,12}$ = 14.19, p < .01; Figure 4e).

3.2.3 | Impacts of nutrient addition on litter decomposition

When decomposed at the surface, roots were the most recalcitrant tissue of *R. taedigera*; whereas stems were the most recalcitrant tissue of *C. panamensis* (Figure 5c,e). Leaves of *R. taedigera* decomposed slower than *C. panamensis* leaves at the surface and below-ground (Figure 5a,d). Leaves decomposed fastest among *C. panamensis* tissues; whereas stems decomposed fastest among *R. taedigera* tissues (Figure 5b,d).

Nitrogen addition increased the below-ground mass loss of both *R. taedigera* and *C. panamensis* leaves by *c*. 10% (Figure 5a,d). However, this effect was not observed when N and P were applied together. Phosphorus addition in isolation slightly reduced mass loss of *R. taedigera* and *C. panamensis* leaves below-ground (Figure 5a,d).

3.3 | Translocation experiment

Mass loss was consistently greater at the site of litter origin ($F_{2,55}$ = 101.48, p < .001; Figure 6). Specifically, mass loss of *R. taedigera* leaves was *c*. 6% higher at the palm swamp site compared to the *R. taedigera* litter translocated to the mixed forest. This pattern was repeated on *C. panamensis* leaves, with mass loss being 9% higher in the mixed forest site compared to the *C. panamensis* leaves translocated to the palm swamp. The HFAI demonstrated a positive effect of 28%.

4 | DISCUSSION

4.1 | Nutrient controls of extra cellular hydrolytic enzyme activities and litter decomposition

As expected, the mixed forest site had lower nutrient availability than the palm swamp site (Figure 2) and we observed strong effects of the nutrient addition on both extractable (i.e. DOC/TDN) and microbial C:N in the low nutrient mixed forest, but not in the nutrient-rich palm swamp (Figure 3). In contrast to our prediction that sites with microbial nutrient limitation would respond to nutrient addition by down-regulating enzymes involved in nutrient acquisition, we found no down-regulation of phosphomonoesterase activity at either site. However, in line with our prediction, the activity of enzymes involved in the decomposition of large plant-derived polymers, including β-glucosidase, arylsulphatase and *N*-acetyl-β-glucosaminidase, were enhanced by N addition in surface peat in the palm swamp and by P addition in the mixed forest, respectively (Figure 4d,e). This reflects differences in the nutrient levels at the two sites: low N relative to P concentrations at the palm swamp and low P concentrations in the mixed forest (Olander & Vitousek, 2000; Sjögersten et al., 2011) and suggests that the degradation of sugars as well as more complex organic molecules in this peatland are in part limited by variation in forest nutrient status in agreement with findings from higher latitude peatlands (Bubier, Crill, Mosedale, Frolking, & Linder, 2003; Wang et al., 2014).

In contrast to our prediction that nutrient addition would accelerate litter mass loss at the low nutrient site, but have little effect, at the high nutrient palm site, N addition increased mass loss of leaf litter deeper in the peat profile by *c*. 10% (Figure 5a,d). This is important because foliar litter inputs represent a sizable fraction (*c*. 30%) of the total C inputs from net primary productivity (333 g C m^{-2} $year^{-1}$; Sjögersten et al., 2014) and partially decomposed leaf litter contributes to long-term C storage in peatlands as it becomes buried and preserved over time due to water-logged conditions (Hoyos-Santillan et al., 2015). Nitrogen addition affected leaf litter decomposition only at depth, indicating that nutrient limitation is an additional constraint on decomposition under anaerobic conditions,

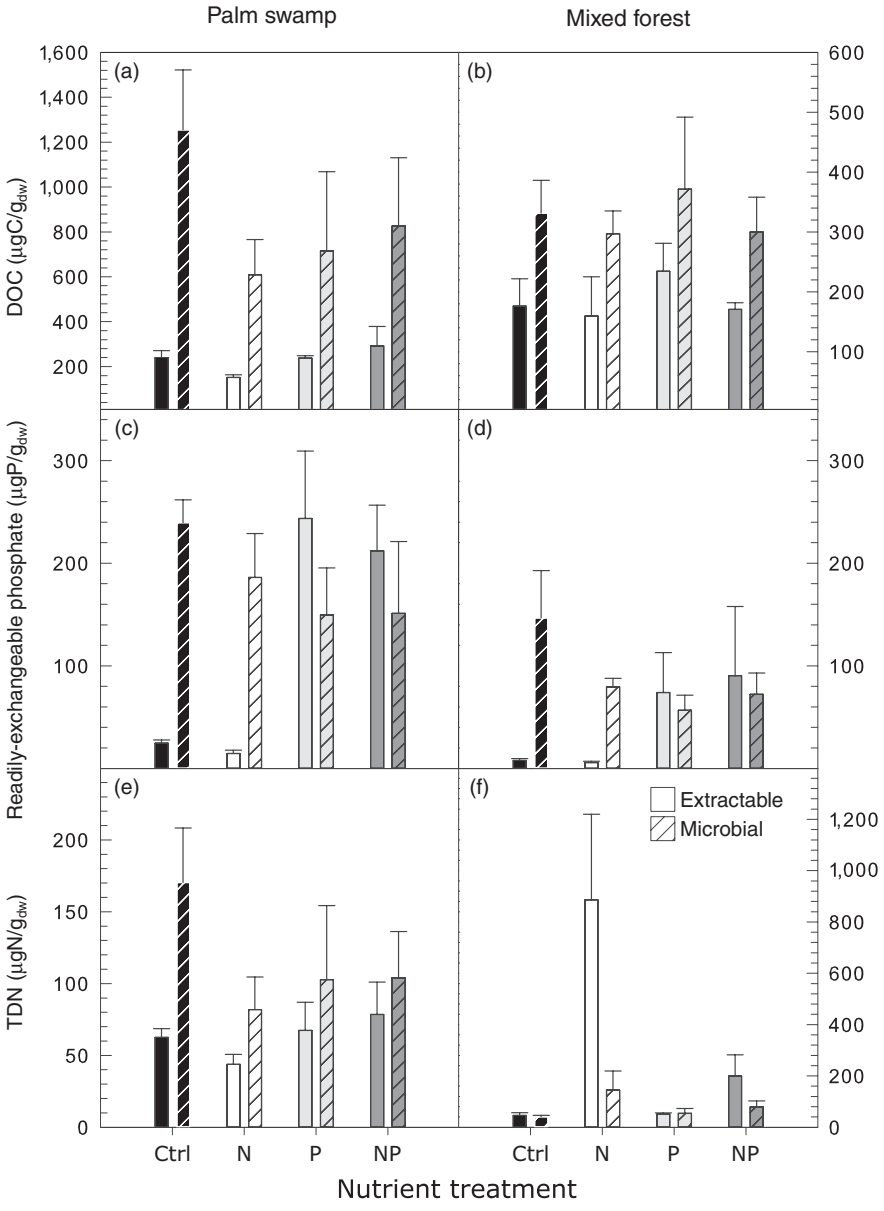

FIGURE 2 Comparison of extractable (solid bars) and microbial (hatched bars) Ctrl, N and P in surface peat at the two study sites, (a, c, e palm swamp; b, d, f mixed forest). Dissolved organic carbon (a, b), readily-exchangeable P (c, d) and total dissolved N (e, f), after 5 months of the in situ nutrient addition. Note the different scales on the ordinate axis when comparing palm swamp and mixed forest. Statistical analyses are presented in the text

and/or that nutrient limitation is more pronounced in deeper, more degraded peat. Furthermore, shifts in the microbial community composition and a reduction in microbial activity in response to anaerobic conditions are likely to slow nutrient mineralization at depth (Jackson et al., 2009).

Variation in mass loss responses to N addition among litter types, with leaves decomposing faster with N addition but roots and stems being unaffected, is presumably linked to differences in litter organic chemistry among tissue types (Hobbie & Vitousek, 2000). For example, root and stem tissues from the two study species contained greater concentrations of lignin than leaves, making them more recalcitrant to decomposition (Hoyos-Santillan et al., 2015). As lignin decomposition is strongly limited by oxygen availability (Zeikus, 1981), it is plausible that aeration was a greater limitation of degradation of lignin-rich roots and stems than nutrient availability, explaining why only decomposition of labile leaf litter tissue was enhanced by the N addition under the water-logged conditions at 50 cm depth.

Phosphorus addition reduced litter mass loss, in contrast to our prediction. This might be linked to suppression of phenol oxidase activity, as suggested by findings from mangrove and mineral soil systems (Keuskamp, Feller, Laanbroek, Verhoeven, & Hefting, 2015; Qi et al., 2016), possibly due to a reduction in fungal activity in response to greater concentrations of mineral P (Hobbie, 2000; Tien & Myer, 1990). As a reduction in phenoloxidase activity may reduce decomposition of complex C (Freeman, Ostle, Fenner, & Kang, 2004), suppression of phenol oxidase activity by P addition in our study might therefore explain the reduction in decomposition in P-treated plots.

Taken together, our findings in part support our hypothesis that nutrient availability influences litter decomposition and activities of extra cellular hydrolytic enzymes. Nutrient addition increased the

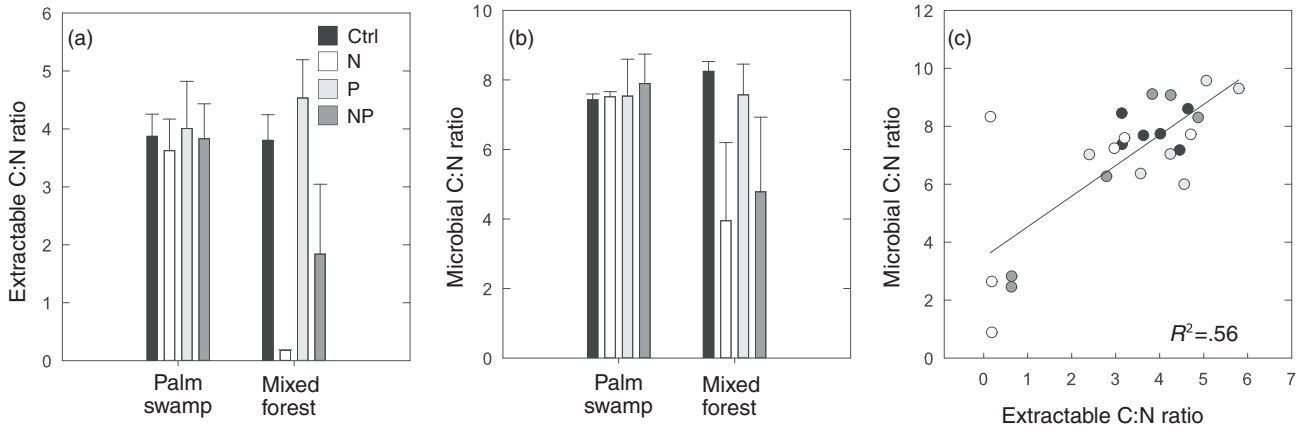

FIGURE 3 Effects of the nutrient addition treatment on the C:N ratio in: (a) the extractable fraction (i.e. DOC/TDN), (b) the microbial biomass and (c) the relationship between the C:N ratio in the extractable fraction and in the microbial biomass. Statistical analyses are presented in the text

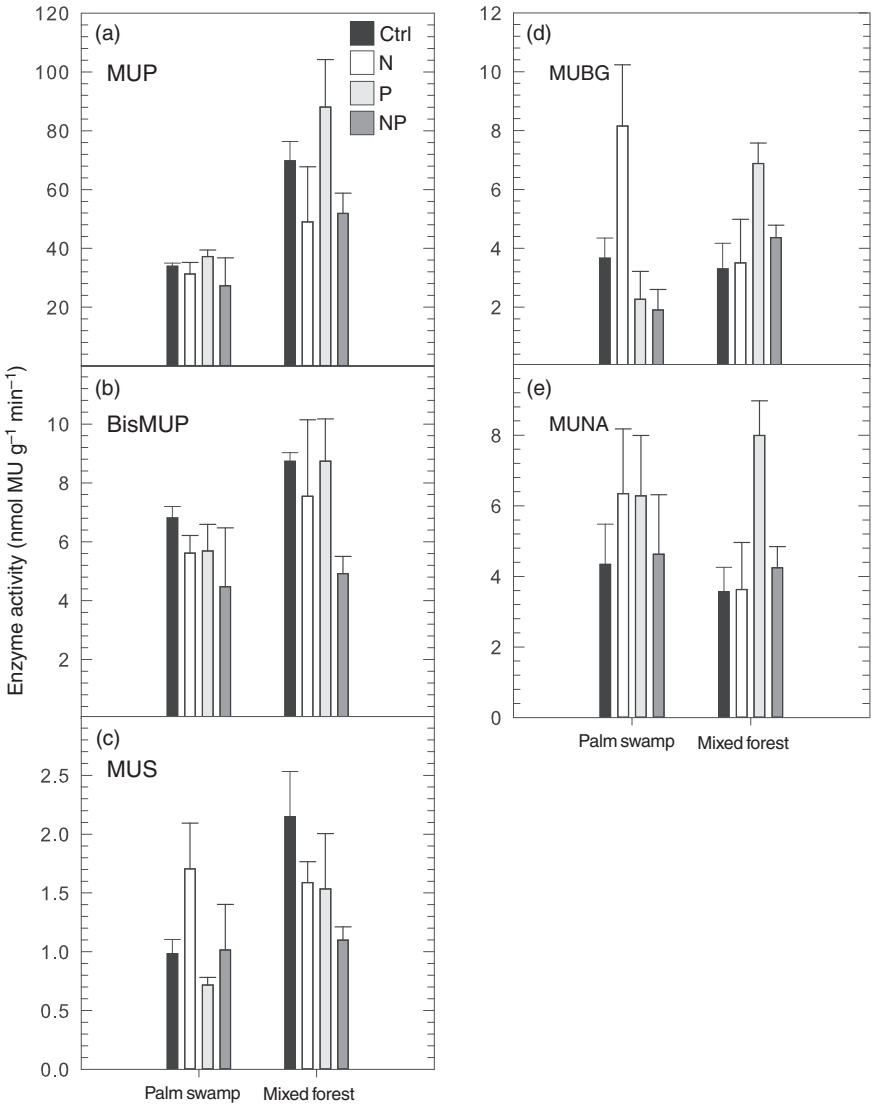

FIGURE 4 Hydrolytic enzymes activity (nmol MU g^{-1} min^{-1}): (a) Phosphomonoesterase (MUP), (b) Phosphodiesterase (BisMUP), (c) Arylsulphatase (MUS), (d) β-glucosidase (MUBG) and (e) *N*-acetyl-β-glucosaminidase (MUNA). Surface peat samples were taken 5 months after the in situ nutrient addition. Statistical analyses are presented in text

activities of extra cellular enzymes involved in degradation of large plant molecules, and increased leaf litter decomposition under anoxic conditions at depth following N addition. However, high C:N or C:P ratios in the bulk litter tissues, relative to low C:N and C:P ratios in the microbial biomass, which are at the lower range of C:N and C:P ratios for the microbial biomass reported in the literature

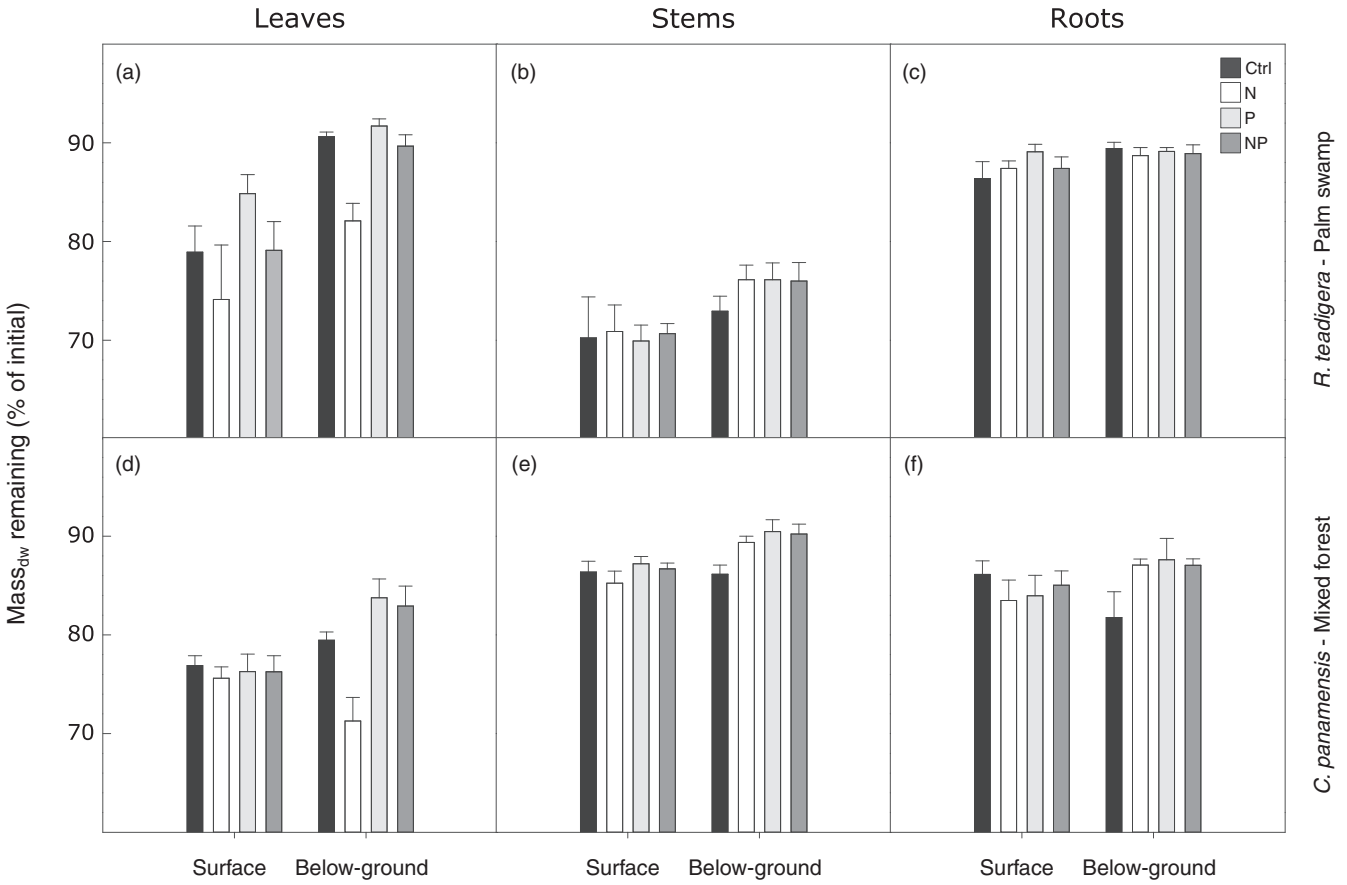

FIGURE 5 Effect of nutrient addition (Control (Ctrl), N, P and N+P) on the in situ % of mass remaining. *Raphia taedigera* litter mass remaining of (a) leaves, (b) stems, (c) roots after 5 months. Residual maximum likelihood (REML) outputs are: Tissue: $F_{2,215} = 121.12$, $p < .001$; Surface/Below-ground: $F_{1,215} = 38.88$, $p < .001$; Treatment: $F_{3,215} = 3.14$, $p < .05$; Tissue × Surface/Below-ground: $F_{2,215} = 7.33$, $p < .001$; Tissue × Treatment: $F_{6,215} = 2.97$, $p < .01$; Surface/Below-ground × Treatment: $F_{3,215} = 0.19$, $p > .05$; Tissue × Surface/Below-ground × Treatment: $F_{6,215} = 0.44$, $p > .05$. *Campnosperma panamensis* litter mass remaining of (d) leaves, (e) stems, (f) roots after 5 months. REML outputs are: Tissue: $F_{2,209} = 95.21$, $p < .001$; Surface/Below-ground: $F_{1,209} = 15.33$, $p < .001$; Treatment: $F_{3,209} = 5.48$, $p < .001$; Tissue × Surface/Below-ground: $F_{2,209} = 0.75$, $p > .05$; Tissue × Treatment: $F_{6,209} = 2.38$, $p < .05$; Surface/Below-ground × Treatment: $F_{3,209} = 4.23$, $p < .01$; Tissue × Surface/Below-ground × Treatment: $F_{6,215} = 3.14$, $p < .01$

(Cleveland & Liptzin, 2007; Xu, Thornton, & Post, 2013), did not predict which litter types were most affected by nutrient addition. Instead, microbial C:N ratios were clearly related to the C:N ratios in the extractable dissolved fraction, suggesting a decoupling between bulk litter chemistry and microbial stoichiometric ratios in line with Fanin, Fromin, Buatois, and Hättenschwiler (2013), although the slope of the relationship shown in this study is steeper. Furthermore, decomposition of leaf litters, which has the lowest lignin:N ratios of the different tissue types (Hoyos-Santillan et al., 2015), was most responsive to N addition. These somewhat contrasting findings suggest that although nutrient availability clearly affects some of the processes controlling litter decomposition in line with stoichiometric theory (Sterner & Elser, 2002), low nutrient availability does not seem to exert a strong control of litter decomposition in these two peat swamp forest communities. Instead, nutrient limitation appears to be mediated by litter chemistry and position in the peat profile, reflecting peat oxygen levels (Hoyos-Santillan et al., 2016).

4.2 | Home field advantage in the context of contrasting site nutrient status

Our findings of a strong positive HFA effect supported our prediction that palm leaf litter would degrade faster at the palm site, while the litter from the low nutrient mixed forest would degrade fastest at the mixed forest site (Figure 6). The HFAI (28%) was at the upper range for HFAI reported in the literature (Ayres et al., 2009; Veen et al., 2015), which we speculate was driven by the two litter species belonging to contrasting plant functional types (i.e. palm vs. evergreen broad leaved), which has previously been shown to result in strong HFA effects and the contrasting site nutrient levels (Ayres et al., 2009; Veen et al., 2015).

Furthermore, the alternative prediction that a site with higher nutrient status would increase litter decomposition rates was not supported by our findings, because *C. panamensis* leaf litter degraded at a marginally greater rate at the low nutrient mixed forest site than the *R. taedigera* leaf litter at the palm site, while root litter decomposition

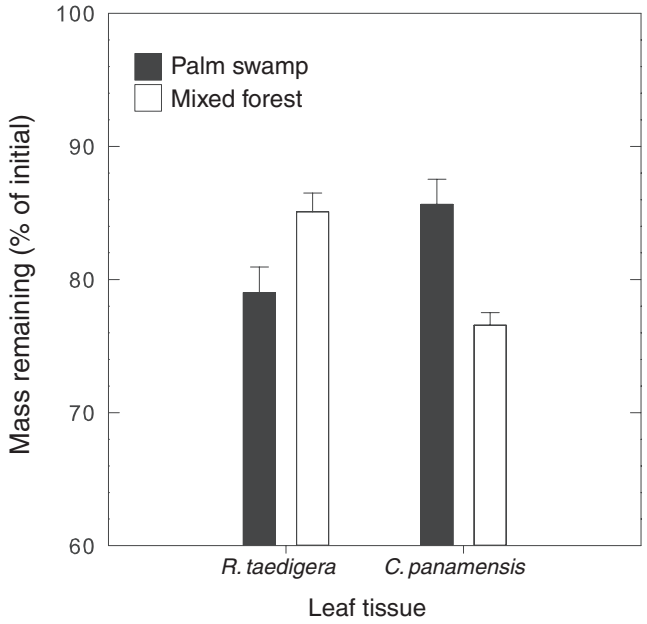

FIGURE 6 Mass remaining (%) of *Raphia taedigera* (palm swamp species) and *Campnosperma panamensis* (mixed forest species) leaf litter after 5 months of decomposition as part of the translocation experiment between palm swamp and mixed forest sites. Litterbags were placed at the peat surface. Statistical analyses are presented in the text

was comparable when incubated at the peat surface (Figures 2 and 5). Although the slower stem decomposition of *C. panamensis* compared with *R. taedigera* might be linked to low nutrient levels at the mixed forest site, contrasting tissue chemistry (i.e. lignified woody vs. palm stem tissue structure) between the two species might also influence decomposition rates (Hoyos-Santillan et al., 2015), as tissue chemistry strongly affects decomposition rates (e.g. Baumann et al., 2009).

The translocation experiment clearly supported the HFA theory. Despite greater fertility at the palm swamp site (Figure 2), which we assumed would enhance decomposition rates, decomposition was always greater for autochthonous litter even when litter was decomposing in the lower nutrient environment. This suggests that the microbial community is adapted to decompose site-specific litter and that a well-adapted decomposer community is more important for decomposition than nutrient availability. This notion is supported by the fact that distinct soil microbial communities accompany particular forest communities within the peatland (Troxler et al., 2012), suggesting that different consortia of micro-organisms are responsible for litter decomposition at the two different sites. This is consistent with previous findings in temperate, subtropical and tropical forests (Austin et al., 2014; Gholz, Wedin, Smitherman, Harmon, & Parton, 2000; Hunt, Ingham, Coleman, Elliott, & Reid, 1988; Mayor & Henkel, 2006; Zhou et al., 2008). For example, it is plausible that different microbial communities produce different enzymes (Kaiser et al., 2014) suggesting that microbial communities involved in decomposition are specialized rather than being functionally redundant (Kaiser et al., 2014; Schimel & Schaeffer, 2012).

4.3 | Peatland C dynamics in the context of nutrient limitation and HFA

Our results indicate that nutrient limitation is an important control of decomposition processes in tropical peatlands and could account for the persistence of relatively labile leaf material deeper in the peat profile where nutrient levels tend to be low (Hoyos-Santillan et al., 2015). However, given that nutrient addition did not accelerate litter mass loss at the peat surface, which is governed by oxic conditions and generally has a faster decomposition rate (Hoyos-Santillan et al., 2015), there does not appear to be a "nutrient latch" on C loss from litter decomposition in this peatland. Our results also support HFA theory, indicating that microbial adaptations to the conditions found at a given site can overcome factors often considered to exert strong controls of litter decomposition rates, such as low nutrient availability.

In the context of long-term peatland carbon dynamics, our study demonstrates that stoichiometric ecological theory applies to peatland decomposition processes, particularly under conditions where oxygen and nutrient levels are low but the organic material is relatively labile (i.e. long-term preservation of leaf litter through the water-logged parts of the peat profile). Our study also suggests that decomposition rates at the peatland surface may remain high across contrasting plant phasic communities as a result of a specialized decomposer communities adapted to these "home" conditions. Finally, our results show that contrasting tissue chemistry should not be used as a predictor of in situ decomposition rates, or different litters contribution to long-term peatland C storage without considering the associated decomposer community at a given site.

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AUTHORS' CONTRIBUTIONS

J.H.-S., B.H.L. and S.S. developed the experimental rationale and defined the methodology; J.H.-S. and S.S. conducted the fieldwork; all authors analysed the data; J.H.-S. and S.S. led the writing of the manuscript; all authors critically evaluated and edited the manuscript and contributed to its completion.

DATA ACCESSIBILITY

Data to support this article are publicly available at Dryad Digital Repository: (Hoyos-Santillan, Lomax, Turner, & Sjögersten, 2017; https://doi.org/10.5061/dryad.460mc).

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