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

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Summary

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 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 remains 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 home field advantage 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 home field advantage 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.

Highlights:

- Nitrogen and phosphorus stimulated activity of hydrolytic enzymes associated with decomposition in agreement with stoichiometric theory.
- Nitrogen availability limited leaf litter decomposition under anoxic conditions, suggesting environmental and litter chemistry controls of nutrient limitation.
- Litter decomposition was greatest at the site where the litter originated, irrespective of site nutrient status, supporting home field advantage theory.

Keywords: carbon turnover, nitrogen, phosphorus, tropical peat, nutrient dynamics

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 microorganisms 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 *et al.* 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 microorganisms (Sterner & Elser 2002; Manzoni & Porporato 2009). 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 (Quested *et al.* 2005; Cornwell *et al.* 2008; Keuskamp *et al.* 2015b). 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; Knorr *et al.* 2005; Keuskamp *et al.* 2013). 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).

Microorganisms 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 (Olander & Vitousek 2000; Allison *et al.* 2007; Sjögersten *et al.* 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 *et al.* 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 approximately 8% greater mass loss when litter material was decomposing at "home" (Ayres *et al.* 2009; Veen *et al.* 2015). However, the effects of the home field advantage 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 (Gorham, Janssens & Glaser 2003; Chimner & Ewel 2005; Dommain, Couwenberg & Joosten 2011) – 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 (Galloway *et al.* 2004; Bragazza *et al.* 2012; IPCC 2013). If

nutrient availability is a key limitation of decomposition in tropical peatlands, as has been found at higher latitudes (Wang *et al.* 2014), then greater nutrient availability might reduce C storage. In addition, nutrient availability shapes the species composition of peat swamp forests (Brady 1997; Page *et al.* 1999; Troxler 2007; Sjögersten *et al.* 2011) and hence the quality and the quantity of litter inputs (Wright *et al.* 2013; Hoyos-Santillan *et al.* 2016), with implications for the composition of the decomposer community (Troxler *et al.* 2012) and decomposition rates (Yule & Gomez 2009; Hoyos-Santillan *et al.* 2015).

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) (Yule & Gomez 2009; Hoyos-Santillan *et al.* 2015). 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; Jackson, Liew & Yule 2009; Hoyos-Santillan *et al.* 2015, 2016). Therefore, decomposition rates of the same litter material differs depending on its position within the peat profile (Hoyos-Santillan *et al.* 2015).

To test the importance of stoichiometric theory (Sterner & Elser 2002; Manzoni & Porporato 2009) 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 (i) activities of extra cellular hydrolytic enzymes, which are involved in microbial nutrient and carbon acquisition and (ii) 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 *et al.* (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 (Kaiser *et al.* 2014; Austin *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

150 2.1. Study sites

151 The study was conducted in the north-west Caribbean coast of Panama where several large
152 peatlands are located within the Bocas del Toro province (Phillips, Rouse & Bustin 1997).
153 Rainfall averages 3092 ± 181 mm yr^{-1}, with a mean annual air temperature of 25.9 ± 0.3 °C
154 (2003 to 2011; Smithsonian Tropical Research Institute Physical Monitoring Program). There is
155 no pronounced seasonality (Wright *et al.* 2011), although there are two periods of reduced
156 rainfall from February to April and August to September.

157 Seven phasic communities have been identified in these peatlands (Phillips *et al.* 1997). We
158 studied two of these: palm swamp dominated by *Raphia taedigera* (Mart.), a canopy forming
159 palm in the Arecaceae family (9°25'29.20"N, 82°24'05.60"W), and mixed forest dominated by
160 *Campnosperma panamensis* (Standl), an evergreen broadleaved hardwood tree in the
161 Anacardiaceae family (9°25'15.00"N, 82°24'14.64"W). The sites were located within the
162 Changuinola peat deposit in the San San Pond Sak wetland (Ramsar site No. 611; ≈ 164 km^2).
163 The distance between the sites was approximately 300 m. Both sites are freshwater (surface
164 water conductivity < 200 µS cm^{-1}), with the water table predominantly at or just below (10 cm)
165 the peat surface. Maximum recorded water fluctuations were + 15 to − 40 cm relative to the peat
166 surface, with surface water consistently above the peat surface during periods of high rainfall.
167 Dissolved O_2 concentrations in the pore water were up to 3.3 ppm at the surface (Palm swamp:
168 1.35 ± 0.25 ppm; Mixed forest: 2.15 ± 0.34), but as low as 0.2 ppm at 50 cm belowground (Palm
169 swamp: 0.72 ± 0.27 ppm; Mixed forest: 0.68 ± 0.19). Nutrient levels at the two sites differ with
170 respect to total and exchangeable P (higher at the palm swamp), as well as microbial N and P
171 (higher at the palm site) and peat C:N and C:P ratios (higher at the palm swamp site) (Sjögersten

172 *et al.* 2011). Palm sites had large amounts of palm leaf litter at the surface and a dense but
173 shallow (1.1 m depth) fibrous root system (Wright *et al.* 2011). The mixed forest sites had large
174 amounts of *C. panamensis* leaf litter at the surface but leaf litter from other species was also
175 present (for further details on of the forest structure and composition see Sjögersten *et al*., 2011
176 and Hoyos-Santillan *et al*., 2016). *C. panamensis* is characterized by woody lignified structural
177 roots reaching at least 1 m depth and abundant surface knee roots (Wright *et al.* 2011).
178 Microtopography within all sites consisted of shallow ponds and raised areas (close to trees
179 associated with root structures).

180

181 2.2. Experimental design and methodology

182

183 *2.2.1. Nutrient addition experiment*

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

191 *R. taedigera* and *C. panamensis* litter for the decomposition study was collected from the palm
192 swamp and mixed forest, respectively. The collected litter consisted of recently senesced leaves,

193 freshly cut leaf stalks (petioles) or stems (~ 5 cm in diameter), and fine lateral roots (2–4 mm
194 diameter) from the top 20 cm of the soil profile. After collection, the litter was cleaned with
195 deionized water (DI) and air dried for five days. To allow comparable masses to be weighed out,
196 the litter material was cut into smaller pieces: leaves were cut into ~ 2 × 2 cm pieces, roots were
197 cut into ~ 2 cm lengths, and stems were cut into ~ 1 cm thick discs to ensure that a cross section
198 of the stem tissue was used. Litter was weighed (leaves: ~ 2 g; whereas stems and roots: ~ 1 g),
199 placed separately into pre-weighed polyester mesh litterbags (10 × 10 cm; 560 μm mesh), and
200 tied with polyamide thread (⌀ = 0.8 mm). Litter bags were placed directly on the peat surface
201 avoiding hollows. For the belowground incubation (50 cm depth), a narrow slit was cut into the
202 peat and litterbags were manually pushed to the right depth. To aid recovery, litter bags were
203 tied to a string which was securely attached to the ground surface. One litterbag of each tissue
204 type was placed at each of the incubations locations at the start of the experiment, giving a total
205 of 480 litterbags (2 depths (surface and 50 cm depth) × 3 tissue types (leaves, stems, roots) × 4
206 nutrient treatments (Ctrl, N, P and N+P) × 2 sites (palm swamp and mixed forest) × 10 blocks).

207 Nutrient enrichment was applied once at the beginning of the experiment by filling 25 cm
208 sections of dialysis tubing (Spectra/Por® membrane: 40mm diameter, 6000 to 8000 molecular
209 weight cut off) with 0.86 mol of either N (Urea: $CO(NH_2)_2$ or P (calcium phosphate monobasic
210 monohydrate: $Ca(H_2PO_4)_2 \bullet H_2O$) fertilizer. This allowed a slow release of nutrients through the
211 membrane (Feller 1995). Within each block, fertilizer was applied at both the surface and
212 belowground (50 cm) adjacent to the litterbags (< 10 cm from litterbags). For the belowground
213 treatment the dialysis tubes were inserted in a narrow vertical slit cut into the peat.

214 After five months, soil samples were collected to evaluate the impact of the nutrient treatments
215 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 one 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 (DON) + 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 h (Sjögersten *et al.* 2011). Extracts were centrifuged (8000 g, 15 min) and DOC and TDN in the supernatant were determined after a five-fold dilution by TOC-TN analyzer (Shimadzu, Columbia, MD). Readily-exchangeable P was determined by extraction with anion exchange membranes (AEM) (Myers, Thien & Pierzynski 1999; Turner and Romero 2009). For this purpose, surface peat (20 g fresh weight) was shaken for 24 h 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 h 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 analyzer (Lachat Quikchem 8500, Hach Ltd, Loveland, CO).

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 *et al.* 1985). Microbial P was determined by extraction by hexanol

239 fumigation and anion-exchange membranes as described previously (Myers *et al.* 1999; Turner
240 & Romero 2009). Microbial P was calculated as the difference between phosphate in fumigated
241 and unfumigated samples.

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

247 To assess if nutrient addition altered the activity of enzymes involved in the release of C, N, P
248 and sulfur from organic compounds, the activities of five different extracellular hydrolytic
249 enzymes were measured at the end of the experiment using fresh surface peat collected from
250 three of the nutrient addition experimental blocks at the palm swamp and the mixed forest.
251 Assays were conducted using methylumbelliferone-linked fluorogenic substrates (Turner &
252 Romero 2009; Turner 2010). Specifically, enzymes and substrates were: i)
253 phosphomonoesterase: 4-methylumbelliferyl phosphate (MUP); ii) phosphodiesterase: bis-(4-
254 methylumbelliferyl) phosphate (BisMUP); iii) arylsulfatase: 4-methylumbelliferyl sulfate
255 (MUS); iv) β-glucosidase: 4-methylumbelliferyl β- D-glucopyranoside (MUBG); v) *N*-acetyl-β-
256 glucosaminidase: 4-methylumbelliferyl *N*-acetyl-β-D-glucosaminide (MUNA). For the assays,
257 peat (2 g fresh weight) was added to 200 mL of 1 mM sodium azide (NaN_3) solution and stirred
258 for 10 min. Aliquots (50 μL) of peat suspension were dispensed into a 96-well microplate
259 containing 100 μL of 200 μM substrate and 50 μL of sodium acetate-acetic acid buffer adjusted
260 to pH 4 (the mean peat pH). Microplates were incubated at 30 °C for 30 min; following
261 incubation 50 μL of 0.5 M NaOH was added to terminate the reaction, and fluorescence was

262 determined immediately on a FLUOstar Optima spectrofluorometer (BMG Labtech, Offenburg,
263 Germany).

264

265 *2.2.2. Litter translocation experiment*

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

272

273 2.2.3. *Litterbag recovery*

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

280

281 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 analyze 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 analyze 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 analyzed 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 home field advantage index (HFAI), which quantifies the extent to which decomposition is faster or slower at home. Results throughout the text and figures are presented as mean ± 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 home field advantage 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 relative mass loss 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. *R. 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 was 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.

325 3.2. Nutrient addition experiment

326

327 *3.2.1. Extractable and microbial nutrients*

328 Five months after the nutrient addition, TDN and readily-exchangeable P were significantly
329 greater in plots where nutrients were applied (N_{add}: $F_{1,28} = 8.71$, $P < 0.01$; P_{add}: $F_{1,56} = 7.67$, $P <$
330 0.01; Fig. 2), apart from TDN concentrations at the palm site. Neither DOC nor microbial C
331 varied significantly with nutrient addition (N_{add}: $F_{1,30} = 1.53$; $P > 0.05$; P_{add}: $F_{1,30} = 0.02$; $P >$
332 0.05). Microbial biomass N and P did not increase in response to the fertilization treatment (N_{add}:
333 $F_{3,6} = 0.87$; $P > 0.05$; $F_{3,6} = 1.16$; $P > 0.05$; at the palm and mixed forest, respectively; P_{add}: $F_{2,11}$
334 $= 1.04$; $P > 0.05$; $F_{2,10} = 1.71$; $P > 0.05$; at the palm and mixed forest, respectively; Fig. 2).
335 However, both the DOC/TDN (*i.e.* the extractable fraction) (Site × N_{add}: $F_{1,12} = 13.66$; $P < 0.001$)
336 and microbial C:N (Site × N_{add}: $F_{1,12} = 5.59$; $P < 0.05$) ratios decreased significantly in response
337 to N addition at the low nutrient mixed forest site (Fig. 3a,b); and there was a positive
338 relationship ($F_{1, 23} = 30.09$; $P < 0.001$; $R^2 = 0.56$) between the DOC/TDN and microbial C:N
339 ratios (Fig. 3c).

340

341 *3.2.2. Impacts of nutrient addition on extracellular enzymatic activity*

342 Phosphomonoesterase activity was higher in the mixed forest site than at the palm swamp site
343 ($F_{1,4} = 58.28$, $P < 0.01$) but was not affected by nutrient addition ($F_{3,12} = 1.95$, $P > 0.05$) (Fig.
344 4a). The activity of phosphodiesterase did not vary between sites ($F_{1,4} = 4.23$, $P > 0.05$) or
345 treatments ($F_{3,12} = 1.9$, $P > 0.05$) (Fig. 4b). Arylsulfatase activity decreased with P addition ($F_{1,12}$

346 = 5.72, $P < 0.05$), while N addition increased arylsulfatase activity at the palm swamp but not at
347 the mixed forest site (Site × N_{add}: $F_{1,12} = 5.5$, $P < 0.05$) (Fig. 4c). β-glucosidase activity did not
348 vary between sites (Fig. 4d), but was increased by N addition at the palm swamp but not at the
349 mixed forest (Site × N_{add}: $F_{1,12} = 4.03$, $P < 0.05$). In contrast, P addition increased *N*-acetyl-β-
350 glucosaminidase activity at the mixed forest but not at the palm swamp (Site × P_{add}: $F_{1,12}$ =
351 14.19, $P < 0.01$) (Fig. 4e).

352

353 *3.2.3. Impacts of nutrient addition on litter decomposition*

354 When decomposed at the surface, roots were the most recalcitrant tissue of *R. taedigera*; whereas
355 stems were the most recalcitrant tissue of *C. panamensis* (Fig. 5c,e). Leaves of *R. taedigera*
356 decomposed slower than *C. panamensis* leaves at the surface and belowground (Fig. 5a,d).
357 Leaves decomposed fastest among *C. panamensis* tissues; whereas stems decomposed fastest
358 among *R. taedigera* tissues (Fig. 5b,d).

359 Nitrogen addition increased the belowground mass loss of both *R. taedigera* and *C. panamensis*
360 leaves by ~ 10% (Fig. 5a,d). However, this effect was not observed when N and P were applied
361 together. Phosphorus addition in isolation slightly reduced mass loss of *R. taedigera* and *C.*
362 *panamensis* leaves belowground (Fig. 5a,d).

363

364 *3.3. Translocation experiment*

Mass loss was consistently greater at the site of litter origin ($F_{2,55}$ = 101.48, P < 0.001) (Fig. 6). Specifically, mass loss of *R. taedigera* leaves was approximately 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 home field advantage index (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 (Fig. 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 (Fig. 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, arylsulfatase 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 (Fig. 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

387 nutrient status in agreement with findings from higher latitude peatlands (Bubier *et al.* 2003;
388 Wang *et al.* 2014).

389

390 In contrast to our prediction that nutrient addition would accelerate litter mass loss at the low
391 nutrient site, but have little effect, at the high nutrient palm site, N addition increased mass loss
392 of leaf litter deeper in the peat profile by ~ 10 % (Fig. 5a,d). This is important because foliar
393 litter inputs represent a sizable fraction (~ 30%) of the total C inputs from net primary
394 productivity (NPP; 333 g C m^{-2} yr^{-1}; Sjögersten *et al.* 2014) and partially decomposed leaf litter
395 contributes to long term C storage in peatlands as it becomes buried and preserved over time due
396 to water logged conditions (Hoyos-Santillan *et al.* 2015). Nitrogen addition affected leaf litter
397 decomposition only at depth, indicating that nutrient limitation is an additional constraint on
398 decomposition under anaerobic conditions, and/or that nutrient limitation is more pronounced in
399 deeper, more degraded peat. Furthermore, shifts in the microbial community composition and a
400 reduction in microbial activity in response to anaerobic conditions are likely to slow nutrient
401 mineralization at depth (Jackson *et al.* 2009).

402 Variation in mass loss responses to N addition among litter types, with leaves decomposing
403 faster with N addition but roots and stems being unaffected, is presumably linked to differences
404 in litter organic chemistry among tissue types (Hobbie & Vitousek 2000). For example, root and
405 stem tissues from the two study species contained greater concentrations of lignin than leaves,
406 making them more recalcitrant to decomposition (Hoyos-Santillan *et al.* 2015). As lignin
407 decomposition is strongly limited by oxygen availability (Zeikus 1981), it is plausible that
408 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 *et al.* 2015a; Qi *et al.* 2016), possibly due to a reduction in fungal activity in response to greater concentrations of mineral P (Tien & Myer 1990; Hobbie 2000). As a reduction in phenoloxidase activity may reduce decomposition of complex C (Freeman *et al.* 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 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 (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 *et al.* (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), were most responsive to N addition. These somewhat contrasting findings suggests 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 (Fig. 6). The HFA index (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 show 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 was comparable when incubated at the peat surface (Fig. 2, 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 affect decomposition rates (*e.g*. Baumann *et al.* 2009).

The translocation experiment clearly supported the HFA theory. Despite greater fertility at the palm swamp site (Fig. 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 microorganisms are responsible for litter decomposition at the two different sites. This is consistent with previous findings in temperate, subtropical and tropical forests (Hunt *et al.* 1988; Gholz *et al.* 2000; Mayor & Henkel 2006; Zhou *et al.* 2008; Austin *et al.* 2014). 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 (Schimel & Schaeffer 2012; Keiser *et al.* 2014).

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

474 the peat profile where nutrient levels tend to be low (Hoyos-Santillan *et al.* 2015). However,
475 given that nutrient addition did not accelerate litter mass loss at the peat surface, which is
476 governed by oxic conditions and generally has a faster decomposition rate (Hoyos-Santillan *et al.*
477 2015), there does not appear to be a "nutrient latch" on C loss from litter decomposition in this
478 peatland. Our results also support HFA theory, indicating that microbial adaptations to the
479 conditions found at a given site can overcome factors often considered to exert strong controls of
480 litter decomposition rates, such as low nutrient availability.

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

490

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Data accessibility

Data to support this article is publicly available at Dryad Digital Repository (Hoyos-Santillan *et al.* 2017; doi:10.5061/dryad.460mc).

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678

679

680 **Table captions**

681 **Table 1** Mass-based ratios among C, N and P in different substrate types at the palm swamp and

682 mixed forest sites.

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*	37.71 ± na	911.5 ± na	24.17 ± na	127.9 ± na	3984 ± na	31.16 ± na
Root*	55.91 ± na	1155 ± na	20.65 ± na	78.19 ± na	1034 ± na	13.22 ± na
Stem*	140.2 ± na	1082 ± na	7.71 ± na	117.8 ± na	963.0 ± na	8.18 ± na
Peat (surface)[a]	41.53 ± na	1142 ± na	45.24 ± na	35.13 ± na	1274 ± na	98.78 ± na
Peat (-50 cm)[b]	19.79 ± na	5642 ± na	196.9 ± na	40.73 ± na	3001 ± na	76.27 ± na

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

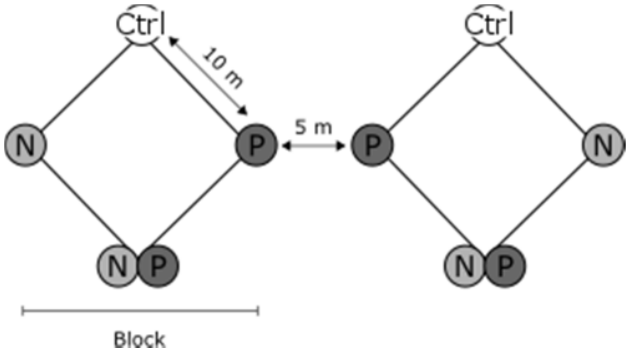
683 **Figure captions**

684 **Figure 1** Schematic diagram outlining the experimental set up for the nutrient addition, (Ctrl)

685 control, (N) nitrogen and (P) phosphorous. The same set up was used at the palm swamp and the

686 mixed forest sites. Ten blocks were set up at each site with litterbags placed both at the peat surface

687 and at 50 cm depth.



688

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.

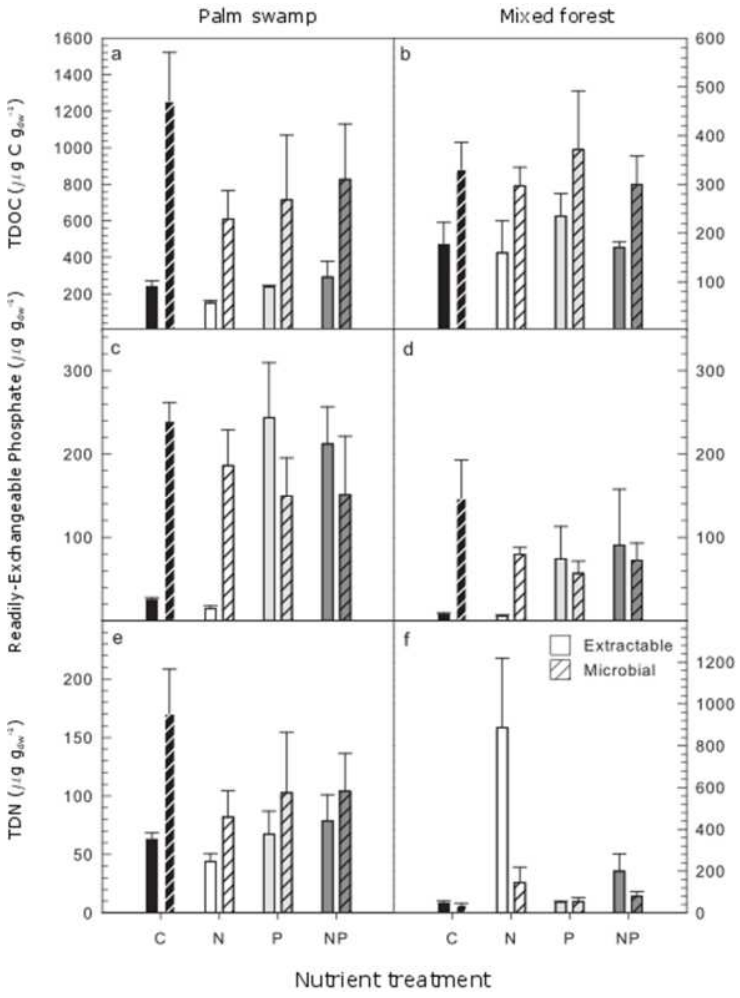


Figure 3 Effects of the nutrient addition treatment on the C:N ratio in: a) the extractable fraction (*i.e.* DOC/TDN), b) the microbial biomass and c) the relationship between the C:N ratio in the extractable fraction and in the microbial biomass. Statistical analyses are presented in the text.

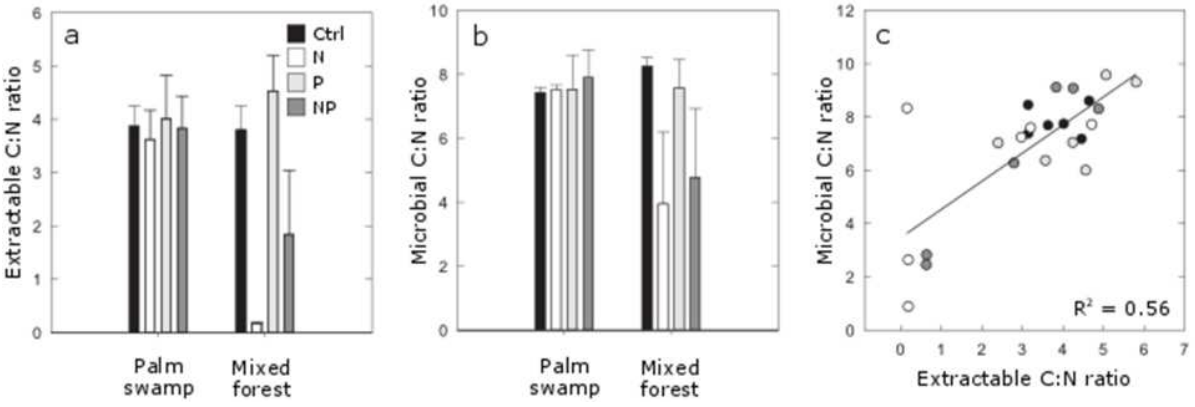


Figure 4 Hydrolytic enzymes activity (nmol MU g^{-1} min^{-1}): a) Phosphomonoesterase (MUP), b) Phosphodiesterase (BisMUP), c) Arylsulfatase (MUS), d) β-glucosidase (MUBG) and e) *N*-acetyl-β-glucosaminidase (MUNA). Surface peat samples were taken 5 months after the *in situ* nutrient addition. Statistical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

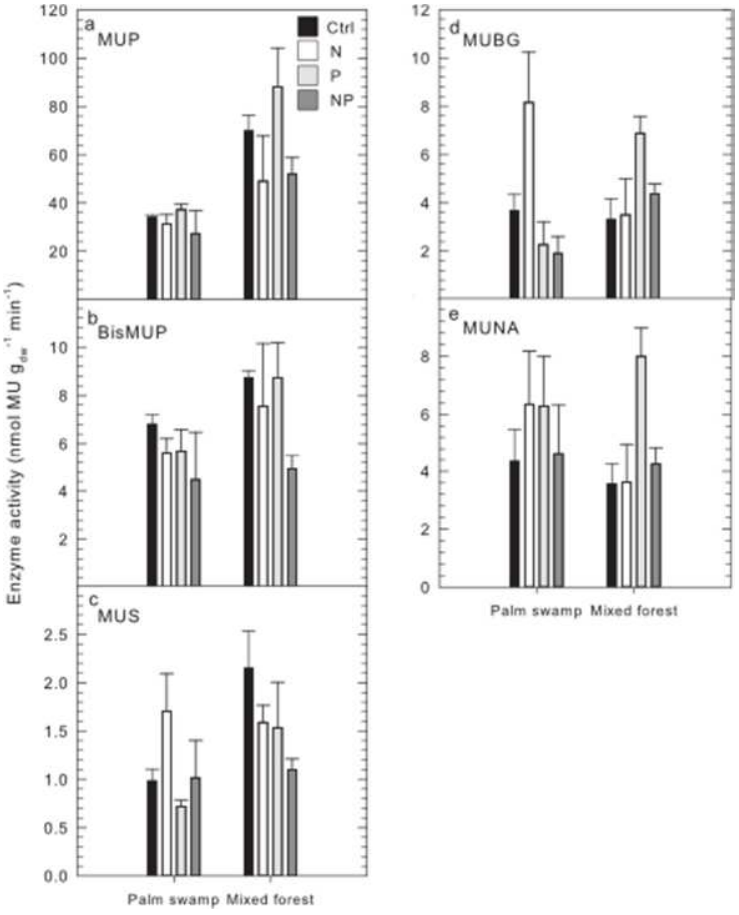


Figure 5 Effect of nutrient addition (Control (Ctrl), N, P and N+P) on the *in situ* % of mass remaining. *R. taedigera* litter mass remaining of (a) leaves, (b) stems, (c) roots after 5 months. REML outputs are: Tissue: $F_{2,215} = 121.12$, $P < 0.001$; Surface/Belowground: $F_{1,215} = 38.88$, $P < 0.001$; Treatment: $F_{3,215} = 3.14$, $P < 0.05$; Tissue × Surface/Belowground: $F_{2,215} = 7.33$, $P < 0.001$; Tissue × Treatment: $F_{6,215} = 2.97$, $P < 0.01$; Surface/Belowground × Treatment: $F_{3,215} = 0.19$, $P > 0.05$; Tissue × Surface/Belowground × Treatment: $F_{6,215} = 0.44$, $P > 0.05$. *C. panamensis* litter mass remaining of (d) leaves, (e) stems, (f) roots after 5 months. REML outputs are: Tissue: $F_{2,209} = 95.21$, $P < 0.001$; Surface/Belowground: $F_{1,209} = 15.33$, $P < 0.001$; Treatment: $F_{3,209} = 5.48$, $P < 0.001$; Tissue × Surface/Belowground: $F_{2,209} = 0.75$, $P > 0.05$;

Tissue × Treatment: $F_{6,209} = 2.38$, $P < 0.05$; Surface/Belowground × Treatment: $F_{3,209} = 4.23$, $P < 0.01$; Tissue × Surface/Belowground × Treatment: $F_{6,215} = 3.14$, $P < 0.01$

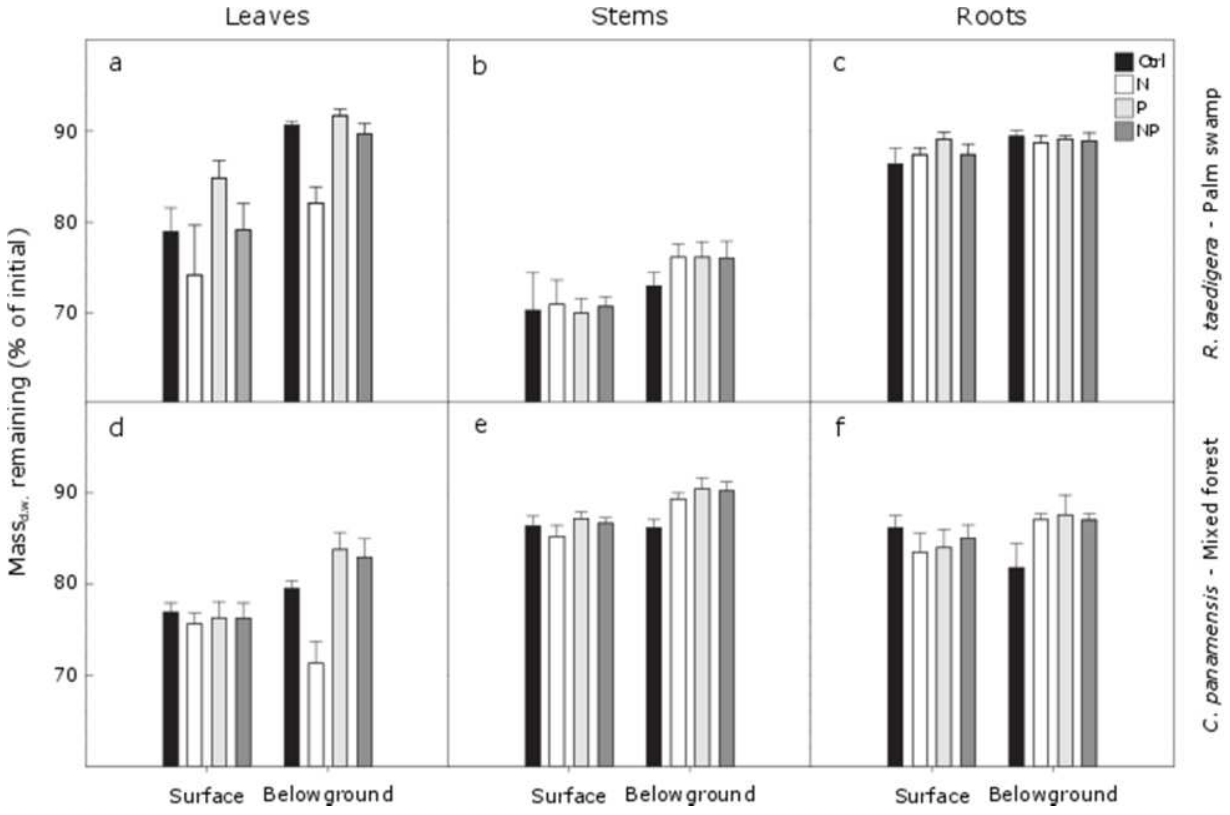
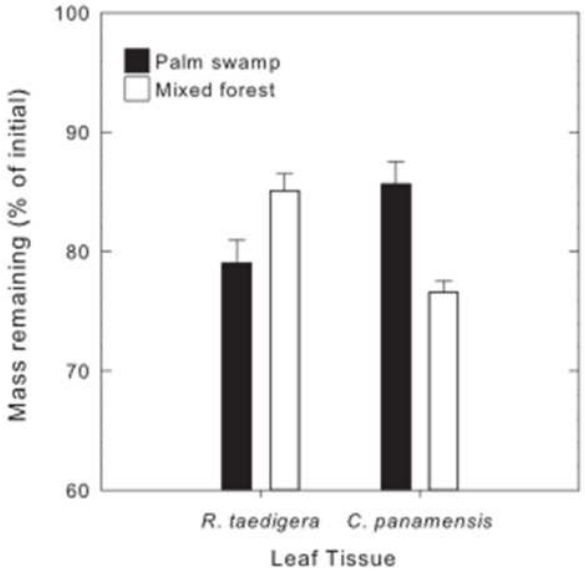


Figure 6 Mass remaining (%) of *R. taedigera* (palm swamp species) and *C. panamensis* (mixed forest species) leaf litter after 5 months of decomposition as part of the translocation experiment between palm swamp and mixed forest sites. Litterbags were placed at the peat surface. Statistical analyses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


100
90
80
70
60
Palm swamp
Mixed forest
Mass remaining (% of initial)
R. taedigera
C. panamensis
Leaf Tissue

722

723