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# Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis

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## Summary

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**Key words:** energy starvation, French Guiana, litter quality, mycorrhizas, nutrient cycling, nutrient limitation, phosphorus, soil fauna.

Proper estimates of decomposition are essential for tropical forests, given their key role in the global carbon (C) cycle. However, the current paradigm for litter decomposition is insufficient to account for recent observations and may limit model predictions for highly diverse tropical ecosystems. In light of recent findings from a nutrient-poor Amazonian rainforest, we revisit the commonly held views that: litter traits are a mere legacy of live leaf traits; nitrogen (N) and lignin are the key litter traits controlling decomposition; and favourable climatic conditions result in rapid decomposition in tropical forests. Substantial interspecific variation in litter phosphorus (P) was found to be unrelated to variation in green leaves. Litter nutrients explained no variation in decomposition, which instead was controlled primarily by nonlignin litter C compounds at low concentrations with important soil fauna effects. Despite near-optimal climatic conditions, tropical litter decomposition proceeded more slowly than in a climatically less favourable temperate forest. We suggest that slow decomposition in the studied rainforest results from a syndrome of poor litter C quality beyond a simple lignin control, enforcing energy starvation of decomposers. We hypothesize that the litter trait syndrome in nutrient-poor tropical rainforests may have evolved to increase plant access to limiting nutrients via mycorrhizal associations.

## Introduction

The ongoing global environmental changes and their consequences for biological diversity are expected to impact the structure and functioning of ecosystems and the services they provide (Millennium Ecosystem Assessment, 2005; IPCC, 2007). Tropical forests are often cast in the spotlight as they stand out as highly significant reservoirs of global

biodiversity (Dirzo & Raven, 2003), and are undergoing particularly rapid change through extensive deforestation (Achard *et al.*, 2002; Mayaux *et al.*, 2005). Their key role in the global carbon (C) cycle has prompted much discussion regarding their importance in climate change mitigation strategies (Gullison *et al.*, 2007; Canadell & Raupach, 2008; Malhi *et al.*, 2008). Such efforts depend on robust predictive models, for which, in turn, proper empirical

estimates of key biological processes of the C cycle, such as photosynthetic C uptake, plant growth and litter decomposition, are essential.

Biogeochemical and global C models are parameterized on the basis of climate variables as drivers of photosynthesis and decomposition, and of plant traits as indicators of ecological and evolutionary constraints on these biochemical and biophysical processes. For example, temperature and moisture functions as well as plant litter quality are used as input variables to predict global decomposition rates and the resulting C fluxes to the atmosphere (e.g. Moorhead *et al.*, 1999; Del Grosso *et al.*, 2005). However, model outputs vary substantially depending on how and which input variables are used (Moorhead *et al.*, 1999; Luckai & Larocque, 2002; Kirschbaum, 2006). Important recent efforts to improve the empirical data for model parameterization have included comparative large-scale and long-term decomposition experiments of global (Parton *et al.*, 2007; Adair *et al.*, 2008; Wall *et al.*, 2008) and regional dimensions (Trofymow *et al.*, 2002) or have focussed on particular ecosystem types such as tropical forests (Powers *et al.*, 2009).

While these recent large-scale experiments spanning multiple ecosystem types have improved the climate component of decomposition models, there remain at least two major limitations to the global empirical databases. First, the contributions of soil meso- and especially macrofauna, key organisms for the regulation of litter decomposition (Lavelle & Spain, 2001; David & Handa, 2010), are rarely assessed in experiments and therefore typically excluded from models despite increasing evidence that their role is particularly important in wet tropical systems (González & Seastedt, 2001; Wall *et al.*, 2008; Coq *et al.*, 2010). Second, the general use of allochthonous litter in these large-scale experiments, be it of one (Wall *et al.*, 2008), two (Powers *et al.*, 2009) or a few (Parton *et al.*, 2007; Adair *et al.*, 2008; Cusack *et al.*, 2009) plant species that do not grow at the experimental incubation sites, may be problematic because the site-specific context under which plant species and their leaf traits evolved, and to which decomposers might have adapted, is lost. Nonnative litter material might decompose at a different rate from locally produced litter characterized by a site-specific syndrome of traits. Moreover, only one or a few introduced litter types might poorly represent local variation in leaf traits and associated decomposition rates which can be even greater than variation in decomposition across broad climatic gradients (Cornwell *et al.*, 2008). Such local variation in leaf traits is particularly important in highly diverse plant communities with low abundances of individual species characteristic of tropical rainforests.

Based on recent findings of ongoing research in a lowland Amazonian rainforest, we discuss here our results in the broader context of drivers of decomposition, offering perhaps some new insights into how plants and decomposers

interactively influence biogeochemical cycling. We aim to revisit the commonly held views that: plant leaf litter traits relevant for decomposition are simply a legacy of live plant functional traits with an accidental influence on decomposition; litter nitrogen (N) and lignin as the two commonly used traits for model parameterization predict litter decomposition in tropical rainforests well; and favourable climatic conditions result in rapid decomposition. We also discuss the importance of fauna to decomposition, a subject of confusion in the literature. Our study site in French Guiana (5°18'N, 52°55'W) within the Amazonian basin is a lowland evergreen primary rainforest composed of *c.* 140 canopy tree species per hectare (Bonal *et al.*, 2008). Total annual precipitation is 2575 mm (10-yr average, 1995–2005) with a drier period, usually < 100 mm month<sup>-1</sup>, from August to November (10-yr monthly average of 68 mm, 1995–2005). There is almost no temperature variation during the course of the year, with an average annual temperature of 25.5°C (10-yr average, 1995–2005). Soils are nutrient-impooverished acrisols (FAO 1998) developed over a Precambrian metamorphic formation called the Bonidoro-series, with a pH of *c.* 4.8 (see Hättenschwiler & Bracht Jørgensen (2010) for detailed soil data). In light of our recent findings, the discussion that follows attempts to understand why there is such high stoichiometric and C quality variation in tropical leaf litters, what the consequence of this variation is for decomposition at our site and for lowland tropical rainforests in general, and what role the soil macrofauna plays in the decomposition process. Finally, we speculate as to whether primary limitation for distinct resources of trees and decomposers may allow complex interactions between organisms in the tropical rainforest community resulting ultimately in strong plant control over the decomposition process.

## The origin of high variation in leaf litter quality

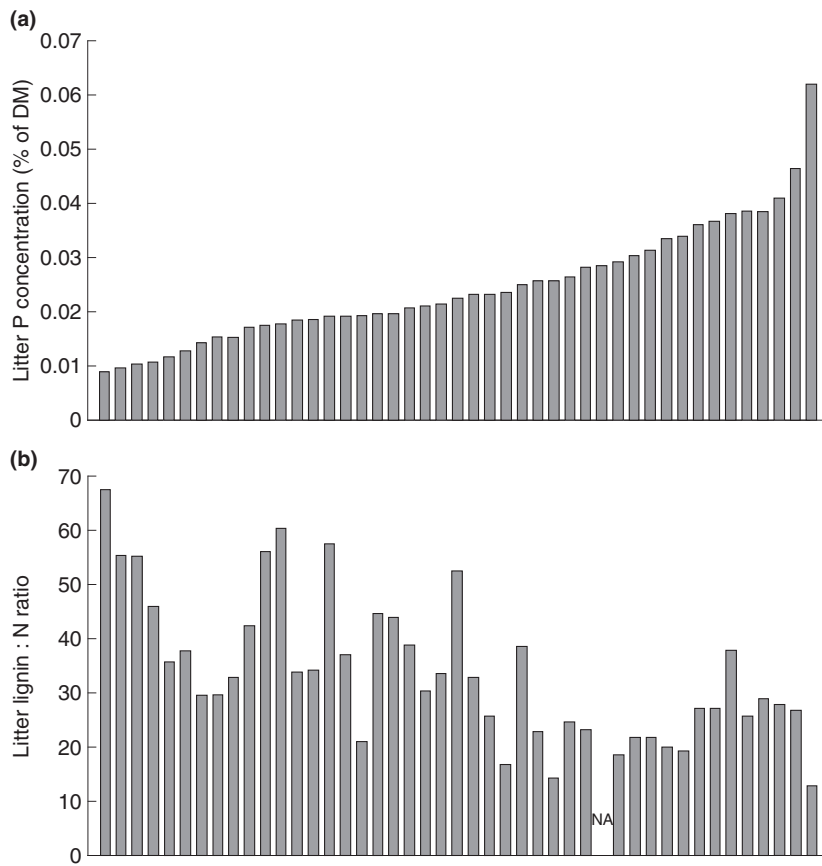
The morphology and tissue chemistry of photosynthesizing leaves are frequently measured plant characteristics that recently have been assembled into large global data sets (Reich & Oleksyn, 2004; Wright *et al.*, 2004, 2005). These global comparisons show an impressively large variation in leaf traits, but nonetheless suggest some large-scale patterns such as increasing leaf N : phosphorus (P) ratios with decreasing latitude (Reich & Oleksyn, 2004) and distinct trait means among plant functional types (PFTs) and plant growth forms (Wright *et al.*, 2004, 2005). Trait variation in green leaves is commonly believed to dictate the variation of the same traits in leaf litter after senescence, with litter quality largely representing this legacy (Cornwell *et al.*, 2008). According to the leaf economics spectrum proposed by Wright *et al.* (2004), plants with leaf traits permitting quick return of invested nutrients and C, that is, high nutrient concentrations and low dry mass investment per leaf area,

also produce leaf litter with high nutrient concentrations and low fibre and lignin contents. Conversely, leaves with low nutrient concentrations and costly dry mass investment per leaf area, that is, slow investment return, produce leaf litter with low nutrient concentrations and high fibre and lignin contents. This legacy of plant functional traits results in plant–soil feedback where plants at the quick end of the leaf economics spectrum produce rapidly decomposing nutrient-rich litter that tends to maintain high soil fertility, and plants at the slow end of the spectrum produce slowly decomposing nutrient-poor litter that reinforces low fertility of soils (Chapin, 1980; Berendse, 1994; Aerts & Chapin, 2000). The correlation between soil fertility and leaf traits has recently been demonstrated at the global scale (Ordoñez *et al.*, 2009). In this first global assessment, leaf P and N concentrations increased with increasing total soil P concentrations across a wide range of ecosystems, but this pattern was less clear with total soil N concentrations or N mineralization rates. Nonetheless, under presumably similar soil P concentrations, the greatest source of variation among plant species remained within-site differences (Ordoñez *et al.*, 2009).

With *c.* 23 mg total P kg<sup>-1</sup> of soil (Hättenschwiler & Bracht Jørgensen, 2010), our study site in the Amazonian rainforest of French Guiana has very low soil P concentrations corresponding to the values reported at the poorest site included in the global comparison by Ordoñez *et al.* (2009). Such low soil P values indicate strongly P-deficient conditions after long-term depletion of P in very old soils (Walker & Syers, 1976; Vitousek *et al.*, 2010) often found in tropical areas, which limit tree growth and net primary productivity in tropical rainforests elsewhere (Vitousek, 1984; Vitousek & Farrington, 1997; Paoli *et al.*, 2005). In agreement with Ordoñez *et al.* (2009), low soil P translated into overall low leaf P concentrations, but only moderately low leaf N concentrations in 45 different tree species co-occurring at our study site (Hättenschwiler *et al.*, 2008). Despite the generally low foliar P concentration, it still varied from 0.037 to 0.116% P (% of total leaf dry mass) by a factor of 3.1 among species. High interspecific variation was also observed for other leaf traits, such as the concentrations of N, lignin, cellulose, hemicelluloses, water-soluble compounds and phenolics (Hättenschwiler *et al.*, 2008). As mostly late-successional evergreen broadleaf trees were sampled within a homogenous area of *c.* 1 ha, climate and soil characteristics as well as PFT-specific traits as the common drivers of variation in leaf traits at larger spatial scales (Aerts, 1996; Cornelissen *et al.*, 1997; Perez-Harguindeguy *et al.*, 2000) could largely be ruled out. It seems that leaf physiology, nutrient use and associated functional leaf traits show strong diversification even at small spatial scales, despite the apparently low variation in environmental factors and the imposed evolutionary constraints related to growth form or PFT. Although the large within-site

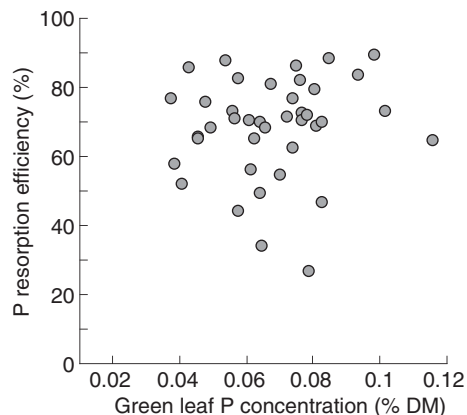
variation of leaf traits has been acknowledged in the broad global comparisons (Wright *et al.*, 2005; Ordoñez *et al.*, 2009), its evolutionary causes and functional consequences beyond apparent differences attributable to growth forms and PFTs are unresolved. The high variation in leaf traits needs to be accounted for, particularly for the highly diversified tropical rainforests, in order to understand its impact on ecosystem processes and how it is influenced by ongoing global change and resulting biodiversity changes (Townsend *et al.*, 2007).

Several harvests of green leaves and freshly fallen leaf litter from the same individuals at our study site indicated that traits generally correlated well between green leaves and litter, and that variation among species remained largely the same in litter compared with green leaves (Hättenschwiler *et al.*, 2008). There was, however, one important exception: P concentration varied much more in litter than in green leaves, with a seven-fold difference between the lowest (0.009% dry mass (DM)) and the highest (0.062% DM) concentrations measured in litter (Fig. 1). Different P resorption efficiencies among species appear to explain the increased variation observed in litter, although P resorption efficiency was unrelated to foliar P concentration (Fig. 2). We estimated an average P resorption efficiency of 70 ± 13% across species, with considerable variation between the species with the lowest (26%) and the highest (89%) P resorption efficiencies (Fig. 2). These results were contrary to expectations of either a fixed minimum amount of P that cannot be withdrawn during senescence (Killingbeck, 1996) or a higher resorption efficiency in species with low leaf P concentrations (Kobe *et al.*, 2005) which would result in either a positive or a negative relationship between resorption efficiency and leaf P concentration. Important consequences are that litter P concentrations cannot be predicted from green leaf P concentrations and that they vary much more than green leaf P concentrations. These results suggest that, while non-labile or poorly labile leaf tissue constituents such as lignin may be mostly a legacy of live leaf functioning once these leaves turn into litter, this is not necessarily the case for labile components such as nutrients, which can be substantially modified by physiological processes during leaf senescence. Corresponding traits in live leaves and leaf litter are even less likely for compounds that are highly labile in both green and senescing leaves, such as nonstructural carbohydrates (NSCs) or low-molecular-weight phenolics. Such C compounds may, however, be of key importance for decomposition, as we will show in the following section. In the set of tree species studied here, litter P concentrations may result from more fundamental strategies for the acquisition and conservation of this rare and growth-limiting nutrient at the whole-tree level. In contrast to P, N concentrations in green leaf and leaf litter were significantly correlated ( $r^2 = 0.55$ , Hättenschwiler *et al.*, 2008). Moreover,



**Fig. 1** Litter phosphorus (P) concentrations (a) and lignin : nitrogen (N) ratios (b) for 45 co-occurring Amazonian rainforest trees (data from Hättenschwiler *et al.*, 2008). Data are presented in the order of increasing litter P concentration with the respective species-specific lignin : N ratio underneath (see Hättenschwiler *et al.*, 2008 for species identities). DM, dry mass; NA, not available.

a lower average N resorption efficiency of  $40 \pm 13\%$ , and litter N concentrations that remained for all but four species above the threshold of 0.7%, indicative of complete N



**Fig. 2** Phosphorus (P) resorption efficiency as a function of green leaf P concentration of the same 45 co-occurring Amazonian rainforest trees presented in Fig. 1 (data from Hättenschwiler *et al.*, 2008). P resorption efficiency was estimated on a unit lignin basis (i.e. total green leaf P and total litter P were calculated per green lignin mass and litter lignin mass, respectively) to account for possible leaf mass changes during senescence (van Heerwaarden *et al.*, 2003). DM, dry mass.

resorption (cf. Killingbeck, 1996), suggest that N is rather a nonlimiting nutrient for tree growth at our study site. P rather than N limitation is also suggested by the mean green leaf N : P ratio of 24.5, which is higher than the threshold of 16 above which biomass production is thought to be P limited (Koerselman & Meuleman, 1996; Aerts & Chapin, 2000). Moreover, litter P concentrations were lower than most values reported previously (Killingbeck, 1996), but similar to the low values reported in eastern Australian ecosystems, which also have very P-poor soils (Wright & Westoby, 2003).

In conclusion, the combined foliage and litter data from individuals of a fairly large number of co-occurring tropical tree species suggest that there is substantial trait variation not accounted for by climatic or soil gradients nor by differences in growth form or PFT. Moreover, some key traits are not simply the legacy of live plant functional traits, but vary beyond and independently of green foliage. Because these traits, such as P concentration in our study system, might have important after-life effects on ecosystem functioning, understanding the evolutionary and ecological drivers of this variation and its functional consequences should be a research priority.

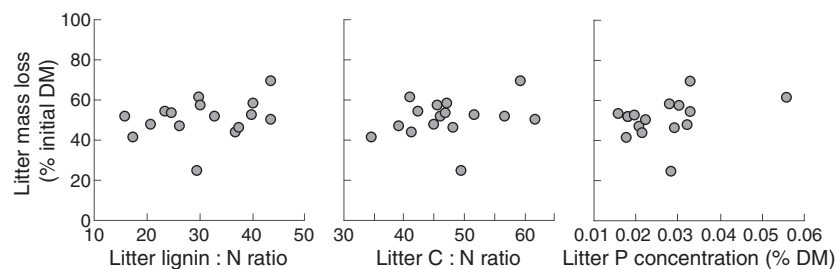
## The consequences of high variation in leaf litter quality

Along with environmental factors, plant litter quality is the major driver of litter decomposition, which in turn plays an important part in the control of the cycling of C and nutrients (Berg *et al.*, 1993; Coûteaux *et al.*, 1995; Aerts, 1997; Moore *et al.*, 1999). When litter quality is kept constant, the climatic variables temperature and humidity explain > 70% of the variation in litter decomposition across large geographical scales (Berg *et al.*, 1993; Coûteaux *et al.*, 1995; Gholz *et al.*, 2000), with particularly rapid decomposition in warm-humid environments corroborating the general perception that the fastest decomposition rates are in tropical rainforests. By contrast, when climatic variables are kept constant, differences in litter quality drive decomposition at a local scale (Melillo *et al.*, 1982; Cornelissen, 1996; Berg, 2000). A recent meta-analysis by Cornwell *et al.* (2008) of a large number of decomposition studies suggested that litter quality actually contributes much more to the overall variability in decomposition than climate. These authors reported an 18.4-fold range in decomposition rates attributable to plant species-specific differences in litter quality compared with the *c.* 6-fold range in decomposition rates for common substrates along the broad climatic gradients covered in the studies of Berg *et al.* (1993) and Parton *et al.* (2007). Variability in N-related litter quality parameters, such as litter N concentration, the lignin : N ratio or the C : N ratio, commonly correlates well with the variability in decomposition rates (e.g. Melillo *et al.*, 1982; Taylor *et al.*, 1989; Moore *et al.*, 1999) and is a widely used predictor for the parameterization of decomposition in biogeochemical models (Moorhead *et al.*, 1999; Nicolardot *et al.*, 2001; Adair *et al.*, 2008).

In view of the well-documented importance of plant litter quality in controlling decomposition, we expected highly variable decomposition rates of litter produced by the diverse tree community at our study site. The litter lignin : N ratio varied between 13 and 67 among the 45

tree species (Fig. 1). Similarly, the litter C : N ratio ranged from 25 to 77 and was mostly driven by differences in N concentration, which varied between 0.68 and 2.01% for the species with the lowest and highest litter N concentrations, respectively (Hättenschwiler *et al.*, 2008). To determine the extent to which litter quality controlled decomposition, litter from a smaller set of 16 different species was exposed in the field using fine mesh bags (0.068 mm) that excluded meso- and macrofauna (Coq *et al.*, 2010). These 16 species covered a somewhat smaller range of litter N concentration (0.75–1.42% DM), lignin : N ratio (16–44), C : N ratio (34–62) and P concentration (0.016–0.056% DM) compared with the larger comparison of 45 species. In contrast to the overwhelming evidence in the literature, the initial lignin : N ratio, C : N ratio, or N concentration explained no variation in litter mass loss after 312 d of decomposition in the undisturbed rainforest (Fig. 3). As previously argued, N is unlikely to be the primary limiting resource in the studied P-poor ecosystem, which may explain the absence of any correlation between litter mass loss and N-related litter quality parameters. However, litter decomposition was also not related to initial litter P concentration (Fig. 3). This result is surprising because of the very low abundance of total soil P, which in this type of highly weathered, ferralitic soils typical of tropical rainforests should mostly occur in an occluded form, not readily available to plants and microorganisms (Walker & Syers, 1976; Vitousek *et al.*, 2010). In comparison, the organic litter P is easily accessible, which should lead to rather rapid exploitation of this resource by soil microorganisms, and thus more rapid decomposition of relatively P-rich litter, as observed in P-limited Hawaiian montane tropical forests (Hobbie & Vitousek, 2000).

Why do the commonly used litter traits predict decomposition so poorly in the studied lowland Amazonian forest? Given that the C : N : P stoichiometry of decomposer organisms differs widely from that of plant litter (Cleveland & Liptzin, 2007; Martinson *et al.*, 2008), they might be limited by the relative availability of these major elements,

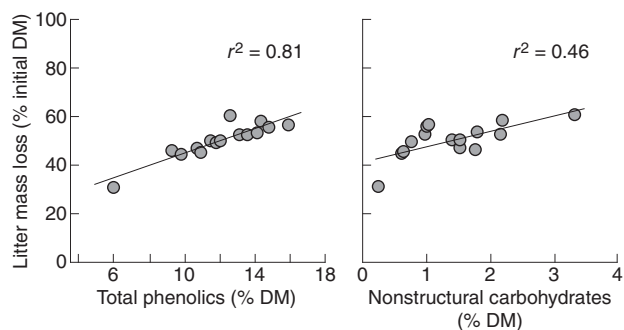


**Fig. 3** Litter mass loss of 16 Amazonian rainforest tree species as a function of initial litter lignin : nitrogen (N) ratio, carbon (C) : N ratio, and phosphorus (P) concentration (data from Coq *et al.*, 2010). Each data point represents the average of four fine-mesh (0.068 mm) litter bags per species exposed in the undisturbed rainforest for 312 d. Simple linear regressions indicated no relationship between mass loss and lignin : N ratio ( $r^2 = 0.08$ ,  $P = 0.30$ ), C : N ratio ( $r^2 = 0.05$ ,  $P = 0.41$ ) or P concentration ( $r^2 = 0.08$ ,  $P = 0.30$ ). Similarly, N concentration alone did not explain any variation in litter mass loss ( $r^2 < 0.01$ ,  $P = 0.87$ ; data not shown). DM, dry mass.



notably by N : P, which is rarely considered as a predictor of decomposition. Hättenschwiler & Bracht Jørgensen (2010) hypothesized that mixtures of litter from several tree species, which is a common feature of the litter layer in the species-rich tropical forest, would provide a stoichiometrically heterogeneous, and thus more favourable substrate than litter from single tree species with a uniform stoichiometry, eventually leading to faster decomposition. However, a field test of this hypothesis using all possible combinations of litter of four tree species from a subset of the pool of 16 species described above, which were distinctly separated along a C : N and a N : P gradient, provided little evidence of stoichiometric control over decomposition (Hättenschwiler & Bracht Jørgensen, 2010).

In contrast to the N- or P-based litter traits, the concentrations of distinct C fractions and groups of C compounds were found to explain a large amount of variation in decomposition (Fig. 4; Hättenschwiler & Bracht Jørgensen, 2010). Labile C compounds such as NSCs and phenolics, which occur in comparatively low concentrations, correlated positively with litter mass loss (Fig. 4). According to our protocol, NSCs consisted of C<sub>6</sub>-sugars and starch, which are easily accessible, energy-rich substrates. These C compounds are not commonly measured in plant litter, probably because they are thought to be depleted completely during leaf senescence or considered unimportant for decomposition because of leaching or immediate microbial breakdown. However, microbial assimilation of easily accessible C substrates might provide the required energy for the production of enzymes that subsequently allow the breakdown of more complex C compounds. This mechanism, known as the 'priming effect', has received quite a lot of attention in the recent literature and is thought to represent an important



**Fig. 4** Litter mass loss of four single litter species and all possible combinations thereof as a function of initial litter concentrations of total phenolics and nonstructural carbohydrates (NSCs) after 204 d of field exposure (data from Hättenschwiler & Bracht Jørgensen, 2010). Each data point represents the average of two fauna exclusion treatments (field microcosms covered with either 0.5-mm or 10-mm mesh; each treatment replicated four times) from a total of 15 different litter treatments. Simple linear regressions were significant at  $P < 0.001$  (total phenolics) and at  $P = 0.006$  (NSCs). DM, dry mass.

pathway of plant-induced decomposition of recalcitrant soil organic matter (e.g. Kuzyakov *et al.*, 2000; Fontaine *et al.*, 2007; Hagedorn *et al.*, 2008). Root exudates and foliage or litter leachates are the most widely discussed sources of priming C compounds for soil organic matter breakdown, but their role in litter decomposition has received little attention. Low-molecular-weight phenolics in litter can act in exactly the same way. However, phenolics are often wrongly considered as inhibiting compounds in the ecological literature and confounded with other groups of polyphenols, such as tannins, that are functionally distinct (Appel *et al.*, 2001) and have different ecological effects (e.g. Schimel *et al.*, 1998; Hättenschwiler & Vitousek, 2000; Coq *et al.*, 2010). In addition to the positively correlated concentrations of NSCs and total phenolics, condensed tannins and lignin correlated negatively with litter mass loss, but not necessarily with each other (Coq *et al.*, 2010; Hättenschwiler & Bracht Jørgensen, 2010), further underlining the importance of the control of litter decomposition by C quality at our study site. While lignin was a quantitatively abundant C fraction, with an average of 32% of initial litter DM, NSCs, total phenolics, and condensed tannins on average contributed only 1.4, 6.5 and 1.5% and did not exceed 4, 14 and 4%, respectively.

In conclusion, decomposition of leaf litter from different tree species with a large range of litter quality suggests that the litter traits commonly used in decomposition models do not predict decomposition in Amazonian lowland rainforests similar to our site. As a consequence, these models would probably poorly assess the impacts of global environmental change on biogeochemical cycles in this important ecosystem. Local deviance from general global models was acknowledged by Adair *et al.* (2008) with a call for testing of site-specific hypotheses regarding the factors controlling litter decomposition in more detail. At our site, there is strong evidence that the quality of C in litter and not the concentration of nutrients controls its decomposition, with faster decomposition of litter types rich in easily accessible labile C compounds and poor in inhibiting compounds. We stress the fact that here 'low litter C quality' does not simply refer to a high content of recalcitrant C ('lignin') according to the traditional use of the term since the seminal works by Swift *et al.* (1979) and Melillo *et al.* (1982), but includes priming compounds such as NSCs and phenolics, and inhibiting condensed tannins of much lower quantities but a disproportional impact on decomposition.

## The key role of fauna

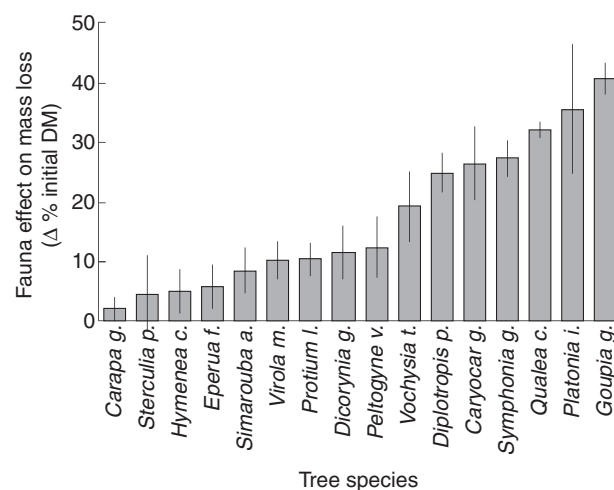
The rich body of literature on the contribution of fauna to decomposition (e.g. Seastedt, 1984; Lavelle & Spain, 2001; Berg & Laskowski, 2006) can be confusing. Confusion arises mainly because of the complexity of soil food webs and regionally very different soil communities which, depending on the researchers' main objectives and their

principal study system, can give the impression of contradictory statements. In addition, ‘decomposition’ is most often broadly used to refer to the disappearance of organic matter, while strictly defined it means the mineralization of organic compounds. Compared with microorganisms, litter-feeding soil invertebrates are commonly assumed to make a minor direct contribution to the mineralization of C and nutrients (Schaefer, 1991; De Ruiter *et al.*, 1993). By contrast, their indirect effects through the consumption and transformation of large quantities of litter material can be substantial (Wolters, 2000; Lavelle & Spain, 2001; David & Handa, 2010). A serious problem for the assessment of fauna effects on decomposition is the inconsistent methodology of field experiments. The widely used litter bag method employs mesh bags that differ substantially in mesh size among studies. The most frequently used 1-mm mesh width, for example, prevents all macrofauna (macroarthropods and earthworms) from entering, but allows access to a large proportion of the mesofauna (mostly dominated by springtails and mites). Depending on the type of ecosystem and its characteristic soil fauna community, these mesh bags yield biased estimates of decomposition and, worse, highly variable biases among ecosystems. As a consequence, the fauna contribution to decomposition is not accurately included in global decomposition models that depend on these empirical field data, which might be the source of a significant amount of the remaining error in model predictions (Wall *et al.*, 2008). The hypothesized strong impact of fauna on decomposition in the humid tropics (Swift *et al.*, 1979) has been confirmed by the few existing studies that have manipulated fauna presence using physical exclusion (using litter bags varying in mesh size) or chemical suppression (naphthalene) across different biomes (Anderson *et al.*, 1983; Heneghan *et al.*, 1999; González & Seastedt, 2001; Wall *et al.*, 2008; Yang & Chen, 2009). The latter three studies used litterbags of  $\leq 2$  mm, and thus accounted specifically for the contribution by microarthropods (mesofauna), but not necessarily macrofauna with larger body sizes.

By using a second set of litterbags of 8-mm mesh size, in addition to the above-mentioned litterbags of 0.068 mm, Coq *et al.* (2010) assessed the combined impact of microarthropods and macrofauna on decomposition at our study site in French Guiana. The average mass loss of litter from 16 different species after 312 d of field exposure was 67.5% when fauna had access compared with 50.1% when fauna was excluded. Although significant, this fauna-driven effect is less impressive than the *c.* 85% mass loss in the presence of fauna (2-mm mesh bags) compared with the 45% mass loss in its absence (0.115-mm mesh bags) reported by Yang & Chen (2009) after 365 d of field exposure in a Chinese tropical rainforest. The discrepancy between the two studies might be related to the contrasting tropical forest ecosystems which are characterized by differing general environmental conditions, possibly associated with differences

in the diversity and abundance of soil fauna. An alternative, nonmutually exclusive reason for the larger fauna contribution in Yang & Chen’s (2009) study compared with that of Coq *et al.* (2010) may be related to the litter types used. While Yang & Chen (2009) used a site-specific litter mixture composed of a variety of species, Coq *et al.* (2010) used single-species litter from a range of different species. The contribution of fauna to decomposition depended strongly on the species identity of the litter (Fig. 5), indicating feeding preferences of fauna and/or litter type-dependent indirect fauna effects on microbial decomposers. The highly significant negative correlation between the fauna effect and litter condensed tannin concentration (Coq *et al.*, 2010) supports the idea that litter palatability and thus choice behaviour of fauna is at the origin of the litter type-specific fauna contribution to decomposition. The way in which fauna influences litter decomposition, however, is unlikely to be simply determined by a rigid relationship between initial litter quality and food choice. The degree to which decomposition of a particular litter type is influenced by fauna has been shown to vary as a function of other litter types present in litter mixtures (Ashwini & Sridhar, 2005; Hättenschwiler & Gasser, 2005) and of interacting fauna species (Heemsbergen *et al.*, 2004; Zimmer *et al.*, 2005; De Oliveira *et al.*, 2010).

In conclusion, soil fauna makes an important contribution to litter decomposition in the studied Amazonian rainforest, supporting the growing evidence of strong animal control of litter decomposition in tropical rainforests



**Fig. 5** Fauna effect on mass loss of litter from 16 different Amazonian tree species after field exposure of 312 d (mean  $\pm$  SE;  $n = 4$ ; data from Coq *et al.*, 2010). The fauna effect is defined as the difference in per cent mass loss between large mesh width litterbags (8 mm) and small mesh width litterbags (0.068 mm). Large mesh width litterbags were double-sided, that is, with the 8-mm mesh covering the upper side, while the lower side facing the soil surface was constructed from 0.5-mm mesh to avoid losses of litter fragments during field exposure. DM, dry mass.



(Wall *et al.*, 2008; Powers *et al.*, 2009). The fauna effect, however, depends on the species identity of the litter and can vary many-fold between preferred and nonpreferred litter types originating from the same forest stand (Fig. 5). A general methodological exclusion of soil fauna, in particular of soil macrofauna, which is commonly achieved by using litterbags of mesh sizes  $\leq 2$  mm and/or by using a restricted number of litter types that do not well represent the typically highly diverse tropical rainforests, may result in wrong estimates of decomposition for tropical rainforests.

### Slow tropical decomposition?

The common paradigm for the tropical forest biome remains that decomposition rates are very rapid. Based on thermodynamically well-defined enzyme kinetics of biochemical reactions, fast process rates in the thermally favourable climatic zone of tropical forests are expected, as long as other potentially limiting factors such as moisture permit. The temperature dependence of heterotrophic soil respiration is described by its  $Q_{10}$  value, the factor by which process rates increase for a temperature increase of  $10^{\circ}\text{C}$ . On average,  $Q_{10}$  values for soil microbial respiration are typically somewhere between 2 and 3 (Raich & Schlesinger, 1992; Kirschbaum, 1995; Fierer *et al.*, 2006; Zheng *et al.*, 2009), which means a 2- to 3-fold higher microbial respiration rate, and thus decomposition rate, with a temperature increase, for example, from  $15$  to  $25^{\circ}\text{C}$ . Accordingly, decomposition of common litter substrates exposed across broad climatic gradients is fastest in tropical rainforests with higher annual mean temperatures than at higher latitudes (Gholz *et al.*, 2000; Parton *et al.*, 2007). In a broad comparative analysis of decomposition in different tropical forests using the same two allochthonous substrate types at all sites,  $> 95\%$  of initial mass disappeared within 1 yr at most sites (Powers *et al.*, 2009). In comparison, the mass loss reported in the different field experiments at our site in French Guiana was slow (Fig. 3, Coq *et al.*, 2010; Hättenschwiler & Bracht Jørgensen, 2010). A possible reason for the much higher decomposition rates reported by Powers *et al.* (2009) might be related to their use of allochthonous plant material of an atypical quality compared with native plant litter. The commercially available leaves of *Laurus nobilis* (probably dried green leaves) used by Powers *et al.* (2009) were low in lignin and were probably quite rich in NSCs, thus providing a more favourable C quality compared with true litter from native species which are additionally often rich in inhibiting condensed tannins (Coq *et al.*, 2010).

Is the comparatively slow decomposition at our site in French Guiana a particular case or does it compare to findings in studies in other tropical forests using native litter material? In Table 1 we summarize a nonexhaustive number of studies from undisturbed or little-disturbed tropical lowland rainforests. Across all these studies from four biogeo-

graphic regions of varying tree species composition and soil type, but relatively high annual precipitation, the average mass loss of litter from native tree species after 312 d of field exposure was  $67 \pm 5\%$ , which surprisingly is identical to the average measured across the 16 species at our study site ( $67 \pm 4\%$ ). This close match suggests that decomposition at our study site represents the average of similar tropical rainforests quite well. However, an important message emerging from the studies surveyed in Table 1 is the large variation in decomposition among species and sites (ranging from 37 to 98% mass loss) despite our restrictive criteria for inclusion. This variation suggests that, even under similarly favourable climatic conditions of year-round high temperatures and high annual precipitation, decomposition in the major tropical forests can be highly variable. This contrasts with the common view of a generally rapid decomposition in this type of tropical rainforest and underlines the importance of considering variation in key ecosystem processes in this biome that are unrelated to climatic factors.

We take the argument one step further by stating that decomposition in tropical rainforests is not necessarily more rapid than in other climatic zones. For example, if we compare mass loss of litter from the four tree species used in the study by Hättenschwiler & Bracht Jørgensen (2010) with that of four temperate forest species studied by Hättenschwiler & Gasser (2005), the difference is surprisingly modest (Fig. 6a). In both studies, litter from native tree species decomposed at their site of origin over exactly 204 d during the humid part of the year using exactly the same experimental protocol (see legend to Fig. 6). Despite the much higher average temperature during the experiment of  $24.8^{\circ}\text{C}$  in the tropical rainforest compared with  $7.2^{\circ}\text{C}$  in the temperate deciduous forest, the average mass loss of 45% in tropical litter was only slightly, but significantly, higher than that of temperate litter (33%;  $P = 0.02$ ). If we now account for the large difference in temperature and its direct impact on reaction kinetics at these two sites, the differences in decomposition change dramatically. Litter mass loss expressed per degree day (Fig. 6b) or adjusted by biome-specific  $Q_{10}$  values (Fig. 6c) is significantly lower in the tropical rainforest than in the temperate forest ( $P < 0.001$ ). This difference is not marginal as the  $Q_{10}$  adjusted litter mass loss of all four tropical species is a factor of 2 lower compared with *Fagus sylvatica*, the most recalcitrant litter type in European temperate forests.

These results suggest that the litters from tree species of the studied Amazonian rainforest share a syndrome of quality traits that provide an exceptionally poor decomposer substrate, leading to extremely slow decomposition. Two lines of evidence support this conclusion. First, microbial biomass in decomposing forest litter across a latitudinal gradient ranging from subarctic forests to the tropical rainforest of French Guiana is on average  $> 3$  times lower at our study site compared with any other forest included in this

**Table 1** Comparison of mass loss rates from litterbag decomposition studies carried out in primary tropical rainforests around the world using local canopy tree litters

Reference	Location	Soils <sup>1</sup>	Rainfall <sup>2</sup> (mm); dry season	Litter type species	Duration (d)	Mesh (mm)	$k$ (a <sup>-1</sup> )	Mass loss <sub>365</sub> (%)	Mass loss <sub>312</sub> (%)		
Our study site (Coq <i>et al.</i> , 2010)	Neotropical Paracou French Guiana	Acrisols	2575; August– November	<i>Carapa procera</i>	312	8 × 8			52.2		
				<i>Caryocar glabrum</i>					73.3		
				<i>Dicorynia guianensis</i>					52.5		
				<i>Diploptropis purpurea</i>					73.5		
				<i>Eperua falcata</i>					67.1		
				<i>Coupia glabra</i>					92.9		
				<i>Hymenaea courbaril</i>					69.2		
				<i>Peltogyne venosa</i>					65.0		
				<i>Platonia insignis</i>					83.5		
				<i>Protium sagotianum</i>					53.9		
				<i>Qualea rosea</i>					82.9		
				<i>Simarouba amara</i>					57.5		
				<i>Sterculia pruriens</i>					57.6		
				<i>Symphonia</i> sp.					77.7		
				<i>Virola surinamensis</i>					82.3		
				<i>Vochysia tomentosa</i>					37.3		
Cleveland <i>et al.</i> (2006)	Neotropical Osa Peninsula Costa Rica	Ultisols	> 5000; January–March	<b>Mean (of 16 species)</b>	300	1 × 1	2.82	94.0	67.4		
				<i>Brosimum utile</i>					91.0		
González & Seastedt (2001)	Neotropical Luquillo Experimental Forest Puerto Rico	Oxisols	3524; no dry season	<i>Cecropia scheberiana</i>	528	76.9	71.4				
				1.8 × 1.6							
Santiago (2010)	Neotropical San Lorenzo National Park Panama	Histosols	3100; January–April	<b>Mean (of 11 species)</b>	744	1 × 1	0.71	<b>50.6</b>	<b>45.3</b>		
Wieder <i>et al.</i> (2009)	Neotropical Golfo Dulce Forest Reserve Osa Peninsula, Costa Rica	Ultisols	> 5000; December–April	Local mixture	230	1 × 1	1.93	85.5	80.8		
				<i>Brosimum utile</i>							
				<i>Cecropia obtusifolia</i>						1.31	73.0
				<i>Ceiba pentandra</i>						0.96	61.7
				<i>Huberodendron allenii</i>						2.58	92.4
				<i>Hyeronima alchorneoides</i>						1.62	80.2
				<i>Inga</i> spp.						0.86	57.7
				<i>Manilkara staminodella</i>						1.62	80.2
				<i>Pouteria lecythidicarpa</i>						0.99	62.8
				<i>Qualea paraensis</i>						1.11	67.0
				<i>Schizolobium parahyba</i>						1.13	67.7
<i>Symphonia globulifera</i>	3.24	96.1									
<b>Mean (of 11 species)</b>	2.13	88.1									
		<b>75.2</b>									

**Table 1** (Continued).

Reference	Location	Soils <sup>1</sup>	Rainfall <sup>2</sup> (mm); dry season	Litter type species	Duration (d)	Mesh (mm)	$k$ (a <sup>-1</sup> )	Mass loss <sub>365</sub> (%)	Mass loss <sub>312</sub> (%)
Anderson <i>et al.</i> (1983) <sup>3</sup>	Indo-Malaya Gunung Mulu National Park Sarawak, Malaysia	Peaty podisols Red- yellow podisols Humus podisols, acidic	> 5000; July–September	Local mixture (Alluvial) Local mixture (Dipterocarp) Local mixture (Heath)	300	7 × 20	0.96 0.72 0.96	61.71 51.32 61.71	56.0 46.0 56.0
Kurokawa & Nakashizuka (2008)	Indo-Malaya Lambir Hills National Park Sarawak, Malaysia	Sand or clay, nutrient poor	2700 no dry season	<b>Minimum value (40 sp.)</b> <b>Maximum value (40 sp.)</b>	168	2 × 2	0.67 4.85	<b>48.8</b> <b>99.2</b>	<b>43.6</b> <b>98.4</b>
Rogers (2002) <sup>4</sup>	Australasia Oomsis Forest, Morobe Papua, New Guinea	Chromic Luvisols (Schist- derived)	3000; no dry season	<i>Pometia pinnata</i> <i>Celtis kajewskii</i> <i>Dysoxylum caulostachyum</i> <b>Mean (of 3 species)</b>	84	1 × 1	1.17 2.12 2.22	69.0 88.0 89.1	63.2 83.7 85.0
Chuyong <i>et al.</i> (2002) <sup>3</sup>	Afrotropic Korup National Park Cameroon	Sandy, nutrient- poor, strongly acidic	5060; December– February	<i>Berberlinia bracteosa</i> <i>Didelotia africana</i> <i>Microberlinia bisulcata</i> <i>Tetraberlinia bifoliolata</i> <i>Cola verticillata</i> <i>Oubanguia alata</i> <i>Strephonema pseudocola</i> <b>Mean (of 7 species)</b>	240	2 × 2	2.51 0.97 1.43 1.27 2.52 3.41 2.64	91.86 62.17 76.02 71.97 91.95 96.69 92.86	88.3 56.4 70.5 66.3 88.4 94.6 89.5

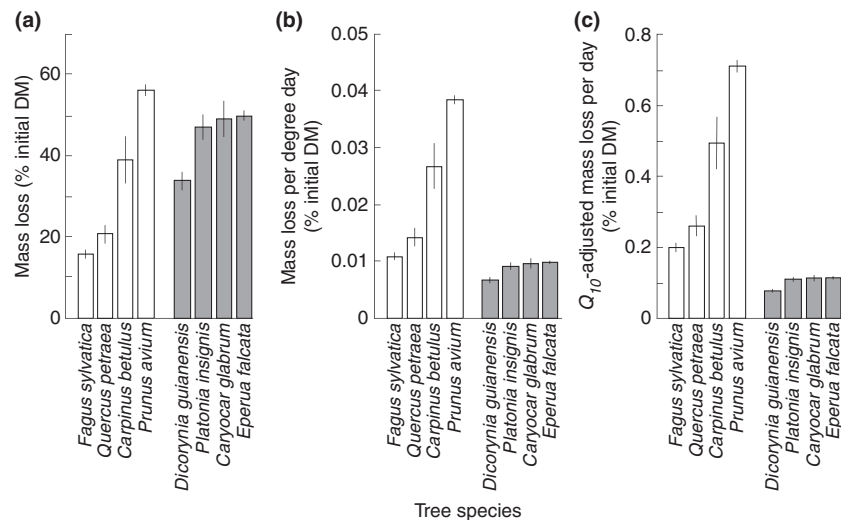
Mass loss (ML) for a duration of 365 days (d) of exposure in the field and for the equivalent duration at our study site of 312 d is calculated using literature-reported decay constants ( $k$ ) and the exponential model  $M = M_0 e^{-kt}$ , where  $M$  and  $M_0$  are the final and original masses, respectively, and  $t$  is time in years (a). Bold letters indicate mean values.

<sup>1</sup>The soil description uses inconsistent nomenclature but summarizes the details as provided by the authors.

<sup>2</sup>Rainfall refers to total annual precipitation as estimated from long-term means.

<sup>3</sup> $k$  values in the original publications were calculated for a  $t$  in months and are expressed here for a  $t$  in years.

<sup>4</sup>Selectively logged 35 yr ago.



**Fig. 6** Litter mass loss of four European temperate forest tree species (open bars; *Fagus sylvatica*, *Quercus petraea*, *Carpinus betulus* and *Prunus avium*; data from Hättenschwiler & Gasser, 2005) and four Amazonian tropical rainforest tree species (closed bars; *Dicorynia guianensis*, *Platonia insignis*, *Caryocar glabrum* and *Eperua falcata*; data from Hättenschwiler & Bracht Jørgensen, 2010). Litter from both sets of species decomposed in its undisturbed mature forest of origin over exactly the same period of time of 204 d during the humid part of the year (November–June). The same experimental set-up of field microcosms with an open bottom and sides covered with 0.5-mm mesh, inserted into the forest floor and filled with homogenized soil of origin, was used in both experiments (only data from single-species microcosms without added fauna are shown;  $n = 3$  and  $n = 4$  (mean  $\pm$  SE) for temperate and tropical species, respectively; see Hättenschwiler & Gasser (2005) and Hättenschwiler & Bracht Jørgensen (2010) for experimental details and site descriptions). (a) Total mass loss as a percentage of initial dry mass (DM) after 204 d of decomposition in the field. (b) Mass loss per degree day (calculated as the sum of all daily mean temperatures above 0°C over the entire experimental period). Temperature was measured continuously at 3-h intervals in both experiments using small temperature loggers placed at the interface of the soil and litter layer in a series of microcosms. The average temperature over the entire experimental period was 7.2 and 24.8°C with 1463 and 5083 degree days in the temperate and tropical experiments, respectively. (c)  $Q_{10}$ -adjusted mass loss per day. Data are calculated at the intermediate temperature of 16°C assuming a lower  $Q_{10}$  of 2.32 in the temperate forest compared with 2.94 in the tropical forest ( $Q_{10}$  values are taken from the broad comparison across different biomes published by Zheng *et al.*, 2009).

gradient (O. Butenschön *et al.*, unpublished data). Second, litters from nonnative tree species originating from different forest ecosystems across the same latitudinal gradient all decomposed more rapidly than native litter exposed in the tropical rainforest of French Guiana side by side (M. Makkonen *et al.*, unpublished data). Even the very slowly decomposing litter from temperate *F. sylvatica* or Mediterranean *Quercus ilex* is broken down more rapidly than the native tropical litter.

In conclusion, leaf litter decomposition in the Amazonian rainforest studied here, and also in other tropical rainforests as suggested in Table 1, proceeds unexpectedly slowly, despite near-optimal temperature and humidity conditions throughout most of the year. Collectively, our data suggest that the reason for such slow decomposition is poor litter quality and, more specifically, energy starvation (low concentrations of labile C) and inhibition (condensed tannins) of decomposer communities. Given the fact that decomposer metabolism is driven by ambient temperature, the constantly high temperatures also demand a constantly high availability of energy-rich substrates for the maintenance of an active and abundant decomposer community. Apparently, the established tree community on which the

heterotrophic soil organisms in essence depend does not easily provide this energy-rich organic material, but rather has evolved a suite of chemical leaf traits that produce a litter that is difficult to break down. While carbon quality seems to play a key role, as we outlined above, the ‘recalcitrance’ of the leaf litter at our study site is unlikely to be explained by a single trait or group of compounds, but is rather the result of a trait syndrome involving several litter constituents or compounds. Such plant litter control of decomposers apparently can very effectively reduce rates of decomposition under climatically favourable conditions. For this reason, decomposition in tropical rainforests is not necessarily very rapid, and the use of common nonnative litter material is likely to be leading to substantial errors in estimates of tropical decomposition rates.

### Linking litter traits, mycorrhizas and decomposers: a new hypothesis

Why do the Amazonian tree species studied produce such slowly decomposing leaf litter? Does the substantial interspecific variation in litter traits and decomposition rates have a functional and evolutionary basis?

As already outlined, patterns of foliage and litter nutrient concentrations and very low soil P all point towards plant P limitation. The little P left in the mineral part of this ancient soil is typically biologically inaccessible (Crews *et al.*, 1995; Vitousek *et al.*, 2010), and plants essentially depend on organic P as the available soil P pool. Plant access to organic P sources is normally mediated by microbial mineralization, but microbial decomposers may initially immobilize most of the mineralized P, especially when soil P sources other than plant-derived organic material are depleted. With faster growth rates, larger surface-area-to-volume ratios, and higher substrate affinities, microorganisms are intrinsically superior competitors for soil nutrients compared with plants (e.g. Kaye & Hart, 1997; Schimel & Bennett, 2004). However, plants can successfully compete with microorganisms by increasing the abundance of nutrient uptake surfaces (roots and associated mycorrhizas) relative to heterotrophic microorganisms, leading to a higher probability of interception of mineral nutrients in time and space (Schimel & Bennett, 2004). Reducing microbial decomposer abundance is a possible way to increase the relative abundance of nutrient uptake surfaces of plants. The litter trait syndrome leading to exceptionally slow decomposition across tree species discussed before appears to efficiently control the abundance and activity of decomposers. The particularly poor decomposer growth substrate produced by the trees could be seen as a potential mechanism to increase plant competitive ability against soil microorganisms for limiting P. However, such decomposer suppression via energy starvation and/or inhibition of secondary compounds such as condensed tannins (Coq *et al.*, 2010) inhibits the very process of mineralization that is fundamental for plant access to mineral nutrients. Mycorrhizal partners that are increasingly recognized for their decomposer capacities (Read & Perez-Moreno, 2003; Finlay, 2008; Talbot *et al.*, 2008) might hold the answer to this dilemma. Consideration of how plants circumvent obligate microbial saprotrophs by direct mycorrhiza-mediated nutrient mineralization or uptake of organic nutrients is important for understanding how plants compete with heterotrophic soil microorganisms for limiting nutrients (Schimel & Bennett, 2004). Strong P limitation in the type of forest studied here might thus have favoured the selection of a decomposer-inhibiting litter trait syndrome and the establishment of efficient nutrient foraging plant–mycorrhizal associations. This ‘litter perspective’ offers an alternative or complementary hypothesis to the ‘green foliage perspective’ of high herbivore pressure and natural selection favouring tannin-rich leaves in tropical trees (cf. Coley *et al.*, 1985; Coley & Barone, 1996). Distinguishing between these evolutionary mechanisms leading to the leaf trait syndrome of tropical trees is an extremely challenging task, and selection for litter rather than foliage traits is certainly more difficult to prove. There is, however,

some convincing evidence for selected litter traits from nontropical ecosystems in the studies by Schweitzer *et al.* (2004) and Wurzbarger & Hendrick (2009), with the latter showing clear involvement of the mycorrhizal partner.

A major counter-argument to the hypothesis proposed here is that neotropical forests appear to be overwhelmingly dominated by arbuscular mycorrhizal fungi (AMF) (e.g. Béreau & Garbaye, 1994; Taylor & Alexander, 2005). Although recent studies reported some decomposer activity and breakdown of organic compounds by AMF (e.g. Hodge, 2001; Atul-Nayyar *et al.*, 2009; Leigh *et al.*, 2009), it is generally accepted that AMF are much less efficient at organic matter breakdown compared with their counterparts from the ericoid mycorrhizal and ectomycorrhizal fungi (EMF) (Read & Perez-Moreno, 2003; Finlay, 2008). However, AMF in association with tropical tree species are poorly studied, and their decomposer capacities are unknown. Moreover, mineralization of P requires a less sophisticated enzymatic capacity than the mineralization of N, because the ester bonds linking P to C can be cleaved with phosphatases without breaking down the C skeleton of organic compounds. Consequently, AMF provided with ample energy from their host trees can proliferate in the soil–litter interface and forage for P, unlike the energy-limited saprotrophs which are dependent on the breakdown of more complex organic compounds.

Despite strong indirect evidence of P limitation at our study site, limitation of a single nutrient is only transitional and simultaneous limitation of P and N, in particular, has been suggested to be common in many ecosystems (Elser *et al.*, 2007; Vitousek *et al.*, 2010). With increasing relative N limitation, the plant competitive advantage over decomposers through the production of recalcitrant litter and investment in AMF might therefore reach its limit. Eventually, trees will have to take up nutrients mineralized by microorganisms with greater enzymatic capacity, such as saprotrophs or maybe EMF. Interestingly, in a rare case in nearby Guiana, the ectomycorrhizal tree species *Dicymbe corymbosa* (Caesalpiniaceae) dominates locally within a diverse AM tree community (Mayor & Henkel, 2006; McGuire *et al.*, 2010). Ectomycorrhizal tree species also occur in African tropical forests (Newberry *et al.*, 1988; Torti *et al.*, 2001). With only a few exceptions, they belong to the same family, Caesalpiniaceae (non N<sub>2</sub>-fixing) (Newberry *et al.*, 1988; Alexander, 1989), and tend to predominate locally over the regionally abundant AM tree species (Newberry *et al.*, 1988; Chuyong *et al.*, 2000; Torti *et al.*, 2001). This striking local dominance of a few EM tree species is probably related to more efficient nutrient acquisition associated with organic matter densely colonized by ectomycorrhizal roots (Newberry *et al.*, 1988). Moreover, our proposed hypothesis of energy starvation/inhibition of decomposer communities competing for limiting nutrients is consistent with slower decomposition and lower



microbial biomass in the neotropical rainforest patches dominated by the EM species *Dicymbe corymbosa* compared with the surrounding species-rich AM tree communities (McGuire *et al.*, 2010). However, if efficient mycorrhizal nutrient competition, especially with an increasing tree N demand, allows EM tree species to achieve local dominance, why is it not more widespread in neotropical forests? The striking absence of EMF from most neotropical forests is even more puzzling given the tremendous success of ectomycorrhizal dipterocarps in South-East Asian tropical forests (Taylor & Alexander, 2005). Perhaps there exist important ecological trade-offs for the type of mycorrhizal association, such as dramatically different constraints for trees as shaded seedlings vs adult canopy trees? Perhaps there are important evolutionary trade-offs or simply chance effects for favourable ectomycorrhizal associations with a particular phylogenetic group of trees, followed by massive radiation such as in the dipterocarps? The fact that Amazonian and African EM tree species occur almost exclusively within the Caesalpiniaceae suggests a strong evolutionary component driving the patterns of EM tree species distribution in tropical rainforests.

Despite selection for a litter trait syndrome imposing important decomposer limitations, there is still substantial variation in leaf and litter traits and decomposition rates among tree species at our study site. This variation suggests that, within general constraints, a multitude of plant strategies exist for successful competition for limiting nutrients. The occurrence of alternative strategies might be better understood within a plant resource allocation framework based on trade-offs between nutrient conservation and nutrient foraging and associated costs. For example, if two opposing gradients from poor to efficient nutrient conservation and from low to high mycorrhizal investment are considered, there may be large numbers of possible ways for trees to separate along these gradients. Such separation along gradients of 'plant nutrition strategies' could eventually contribute to the understanding of the coexistence of high numbers of tree species competing for the same limiting resource. However, the paucity of knowledge on nutrient conservation, rooting patterns, allocation to mycorrhizas of either type, and their saprotrophic capacity currently limits our ability to understand potential trade-offs and alternative strategies of nutrient conservation and foraging in Amazonian tree species.

In conclusion, we hypothesize that, in the neotropical rainforest studied, natural selection favoured a leaf litter trait syndrome that leads to starvation/inhibition of decomposers, thereby increasing the trees' ability to compete for the uptake of highly limiting nutrients, P in particular, via mycorrhizal associations. Our considerations suggest that plants, mycorrhizas and decomposers interact in a complex triangular relationship that in addition may include species-specific interferences between mycorrhizal and saprotrophic

fungi (Gadgil & Gadgil, 1971; Finlay, 2008). This triangular relationship, the distinct properties and accessibilities of the two key nutrients N and P, and their distinct conservation within trees provide a multitude of alternative plant nutrient conservation and foraging strategies. We recognize that our 'decomposer starvation' hypothesis is a preliminary idea that requires thorough theoretical and empirical testing. Such tests might initially focus on the relationships between species-specific litter quality, including a detailed analysis of various C-compounds not commonly assessed, and the respective colonization of this litter by saprotrophic microorganisms and mycorrhizal roots and hyphae. A next step might be detailed characterization of the tree species-specific identity and extent of mycorrhizal associations of Amazonian trees and their saprotrophic capabilities, allowing a more specific test of the stated hypothesis. Simultaneous broad screenings of mycorrhizal associations, leaf longevity, and nutrient resorption additionally might reveal interesting patterns that may improve our understanding of general plant nutrient conservation and foraging strategies and their potential implications for the evolution and coexistence of the high tree species diversity found in these forests.

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