Diversité des litières et cycles biogéochimiques en forêt tropicale humide

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Résumé

Malgré l'importance reconnue des forêts tropicales humides dans la régulation du climat et du cycle global du carbone, la biogéochimie des forêts tropicales reste moins bien appréhendée que celle des autres biomes. En particulier, il existe encore de larges incertitudes quant aux limitations nutritives des processus écosystémiques ou encore sur le rôle de la biodiversité pour les cycles biogéochimiques. La diversité spécifique élevée des arbres de forêt amazonienne se traduit localement par une forte hétérogénéité de la qualité des apports de litière foliaire, ces apports constituant une ressource primordiale d'énergie et de nutriments pour les communautés d'organismes hétérotrophes du sol. Cependant les conséquences d'une telle hétérogénéité des litières foliaires pour le fonctionnement souterrain sont encore peu connues dans ce milieu.

L'objectif de cette thèse est d'établir une compréhension mécaniste des effets de la qualité des apports de litière ainsi que du rôle de leur diversité sur la décomposition. J'ai combiné des fertilisations factorielles de carbone (C), d'azote (N) et de phosphore (P) à l'utilisation d'une large gamme de stœchiométrie C : N : P des litières (issues de différentes espèces d'arbres) en forêt tropicale de Guyane française et en laboratoire pour évaluer la nature et l'étendue des contraintes énergétiques et nutritives imposées par la qualité des litières sur les activités des décomposeurs et la décomposition. Bien que la perte en masse des litières dans ce système d'étude apparait largement expliquée par la qualité des différentes formes de C des litières, suggérant un fort contrôle de la disponibilité en énergie sur la décomposition, les ajouts externes de C n'ont pas permis de mettre en évidence cette apparente contrainte énergétique. Cependant, je montre que la décomposition des litières tropicales est limitée conjointement par N et P, et que l'amplitude de cette co-limitation est fortement reliée à la disponibilité en P des litières ainsi qu'à leur stœchiométrie N : P. Ainsi, même si le P apparaît plus profondément limitant dans ce système (en accord avec l'hypothèse généralement admise d'un fort déficit en P en forêt tropicale humide), l'accès à l'N foliaire semble également contraindre la décomposition.

Je mets également en évidence des effets positifs de diversité des mélanges de litières sur la décomposition, largement amplifiés par la présence de la faune détritivore. De plus, en présence de faune, il apparait qu'une forte dissimilarité stœchiométrique dans les mélanges de litières favorise ces effets positifs. Finalement, je montre que ces effets de diversité des litières sont renforcés à travers les effets à long terme des apports de litières issues des différentes espèces d'arbres contribuant à ces mélanges. Ce résultat suggère que la complémentarité de l'utilisation des ressources émerge à travers des interactions à long terme entre les arbres et les organismes décomposeurs. Cette thèse met ainsi en évidence que la diversité fonctionnelle des arbres, *via* la qualité de leurs litières module la décomposition et donc le recyclage des nutriments et le cycle du carbone en forêt Amazonienne de Guyane française.

Mots clés : forêt Amazonienne, décomposition des litières, stœchiométrie C : N : P, énergie, diversité fonctionnelle

Abstract

Tropical rainforests play a key role in regulating Earth's climate and global carbon cycle. Although their global importance is well-recognized, the factors that are controlling ecosystem processes and the role of biodiversity for the functioning of these ecosystems are less understood than for other biomes. The high tree species diversity in Amazonian rainforests translates into a high variation of leaf litter quality input to the soil. These inputs represent a major resource of nutrients and energy for heterotrophic soil organisms. However the consequences of tree diversity driven heterogeneity in leaf litter quality for belowground processes are poorly studied.

In this PhD thesis, I aim to develop a better mechanistic understanding of how leaf litter diversity and associated heterogeneity in litter quality drives decomposition in the tropical rainforest of French Guiana. With a factorial fertilization experiment adding carbon (C) in the form of cellulose, nitrogen (N), and phosphorus (P) in all possible combinations, and the use of a wide range of leaf litter C : N : P stoichiometries, my goal was to identify the nature and the extent of energetic and nutritional constraints on decomposer activity. Despite an apparent litter C quality control over decomposition, suggesting energy limitation on decomposition, external cellulose additions did not alleviate the supposed energetic constraint. However, litter decomposition was conjointly limited by N and P, with initial leaf litter P and N:P stoichiometry as the dominant litter trait determining the extent of this NP co-limitation. Thus, even if P seems to be the key limiting factor in our study system (in accordance to the often stated P deficiency hypothesis in many tropical rainforests), the access to N seems also to play an important role in controlling decomposition.

Litter diversity effects on decomposition of litter mixtures were mostly positive and they were particularly strong in the presence of soil fauna and with increasing stoichiometric dissimilarity of the litter mixtures. These positive litter mixture effects on decomposition were also reinforced with the long-term presence of individuals of the tree species contributing to the litter mixtures. This result suggests that complementarity effects in mixed litter decomposition may emerge through long-term interactions between aboveground and belowground biota. Collectively, this PhD thesis showed that functional diversity of trees, *via* their leaf litter quality and resource availability in the environment influences decomposition, and thus affects the carbon and nutrient cycles in this Amazonian rainforest of French Guiana.

Key-words: Amazonian rainforest, litter decomposition, C : N : P stoichiometry, energy, functional diversity

Introduction

"Clearly a remarkably intricate interplay and continuous feedback among the hydrosphere, atmosphere, biosphere and solid substrate must exist. Until we understand both qualitatively and quantitatively the interconnectedness of the many Earth systems, conscious human modification of the planet will be rather analogous to a five-year-old trying to repair a Swiss timepiece"

(Ernst, 2000)

La vie sur Terre est possible grâce à une vingtaine d'éléments chimiques qui, ensemble, forment une formidable diversité de molécules plus ou moins complexes (Sterner & Elser, 2002). Les sources de ces éléments chimiques indispensables à la vie se situent dans la croûte terrestre, l'hydrosphère et l'atmosphère et, les processus biologiques sont ainsi étroitement liés aux échanges des éléments entre ces différents réservoirs. La définition même de la vie implique que les organismes ne se contentent pas de vivre passivement dans leur milieu, et c'est au travers de l'ensemble de leurs activités et des flux générés qu'ils participent au transfert, tous les ans, de plusieurs centaines de millions de tonnes d'éléments et de composés entre l'atmosphère, l'hydrosphère et la lithosphère (Naeem *et al.*, 2002). Les cycles biogéochimiques correspondent à cette circulation permanente des éléments chimiques entre biosphère et géosphère, et sont ainsi fondamentaux pour le maintien et la régulation du fonctionnement de l'ensemble des écosystèmes de la planète : ils déterminent la viabilité des écosystèmes, des biomes et donc de la planète Terre (Lovelock, 1979; Schlesinger, 1997).

Dans ce vaste ensemble qu'est la Terre, la biosphère est un système incroyablement diversifié, complexe et dynamique, incluant 10 à 100 millions d'espèces, résultant d'une histoire évolutive de 3,5 billions d'années (Dirzo & Raven, 2003). Au cours de cette évolution, les espèces ont modifié leur environnement, lequel a lui-même façonné la diversité du vivant

(Laland *et al.*, 1999). Par conséquent, pour comprendre la complexité du fonctionnement[1] des écosystèmes terrestres, il faut non seulement comprendre les cycles biogéochimiques, mais aussi le rôle que joue la biodiversité[2] dans ces cycles.

Dans une vision simplifiée, le fonctionnement d'un écosystème terrestre s'articule autour de 3 composantes (Swift *et al.*, 1979) : les producteurs primaires, le système des herbivores, et celui des décomposeurs. L'intégrité d'un écosystème est maintenue par le transfert d'énergie et de matière entre ces trois compartiments. Les producteurs primaires (les plantes dans les écosystèmes terrestres) constituent la brique de base du fonctionnement des écosystèmes, en convertissant et en stockant l'énergie solaire sous forme de matière organique (via leur activité photosynthétique), et en prélevant dans le sol les éléments minéraux essentiels à leur croissance. L'énergie chimique potentielle et les nutriments stockés dans la biomasse des producteurs primaires sont ensuite redistribués à l'ensemble des réseaux trophiques aériens et souterrains, via les herbivores (consommateurs de la biomasse vivante des producteurs primaires) et les saprophages (consommateurs de la matière organique morte issue principalement des producteurs primaires). La décomposition de la matière organique morte est le seul processus écosystémique permettant un recyclage massif des nutriments, les rendant de nouveau disponibles pour la nutrition des plantes et des micro-organismes. Ainsi, production primaire et décomposition sont des fonctions fondamentales des écosystèmes, fournissant nourriture et habitat pour l'ensemble des communautés aériennes et souterraines. Quel que soit l'écosystème considéré, des forêts tropicales arborant une diversité biologique exceptionnelle aux communautés de lichens en Antarctique extrêmement pauvres en espèces, ces processus centraux du fonctionnement des

[1] Le terme de fonctionnement d'un écosystème regroupe souvent différentes notions dans la littérature, en lien avec les biens et les services générés par les écosystèmes (propriétés d'un écosystème qui ont directement une valeur marchande ou qui influencent directement ou indirectement le bien-être humain). Dans la thèse, le terme de fonctionnement se réfère à sa définition première : l'ensemble des flux de matière et d'énergie au sein d'un écosystème.

[2] Le terme *biodiversity* (contraction de *biological diversity*) a été inventé par Walter G. Rosen en 1985. La biodiversité peut être définie comme la variabilité de la vie dans toutes ses formes et à toutes les échelles d'organisation du vivant : diversité génétique, diversité spécifique, diversité écologique (diversité des écosystèmes, des paysages).

écosystèmes sont maintenus. Cependant, leur intensité varie largement dans l'espace et dans le temps, en fonction d'un ensemble de facteurs de contrôles abiotiques (climat, fertilité des sols…) et biotiques (nature et structure des communautés biologiques), en étroite interaction. Comprendre, quantifier et prédire l'évolution des processus écosystémiques, tout en intégrant la complexité des relations que les organismes entretiennent entre eux et avec leur environnement physico-chimique, ainsi que la diversité des formes de vie, sont des enjeux fondamentaux dans l'étude des systèmes biologiques.

L'objectif principal de cette thèse est d'appréhender le rôle de la diversité fonctionnelle des producteurs primaires sur la décomposition des litières en forêt Amazonienne. La première partie de cette introduction présente le cadre conceptuel et général de la relation entre diversité et fonctionnement des écosystèmes. La deuxième partie présente le processus étudié, la décomposition, et notamment les différents facteurs de contrôles. La ressource organique issue des producteurs primaires fournit l'énergie et les nutriments nécessaires aux activités des décomposeurs, mais, suivant sa qualité, elle peut imposer d'importantes contraintes nutritionnelles. La troisième partie présente donc plus généralement le concept de limitation en ressources nutritives, et notamment comment il peut être intégré dans une approche conceptuelle et synthétique visant à considérer le rôle de la stœchiométrie des éléments carbone (C), azote (N) et phosphore (P) dans les interactions trophiques. Enfin, la quatrième partie de cette introduction dresse un portrait du contexte biogéochimique spécifique aux forêts tropicales humides.

I. La biodiversité comme moteur du fonctionnement des écosystèmes

"A greater absolute amount of life can be supported [...] when life is developed under many and widely different forms, [...]

the fairest measure of the amount of life being probably the amount of chemical composition and decomposition within a given period."

Darwin (1859) On the origin of Species

L'idée d'une relation possible entre la diversité en espèces et le fonctionnement d'un écosystème a été énoncée pour la première fois il y a plus de 150 ans par Darwin, dans « l'origine des espèces » (Darwin, 1859). À partir des résultats d'une expérimentation dans laquelle des espèces végétales étaient cultivées en monocultures ou en mélanges, Darwin mentionnait que les combinaisons de plusieurs espèces de graminées favorisaient une plus forte productivité primaire ainsi qu'une décomposition plus rapide. Cependant, ce n'est qu'au cours des années 90, à la lumière du taux alarmant d'extinction des espèces, que le rôle de la diversité dans le fonctionnement des écosystèmes est devenu l'une des questions centrales de la recherche en écologie.

L'extinction des espèces est un phénomène qui se produit depuis que la vie existe. Mais le rythme actuel de la disparition des espèces à l'échelle planétaire correspond à une crise considérée comme l'un des six événements majeurs d'extinction dans l'histoire de la vie (Pimm *et al.*, 1995; Dirzo & Raven, 2003; Pereira *et al.*, 2010). Tandis que les causes d'extinctions lors des crises passées résultent probablement de changements soudains de l'environnement physique (causés par des facteurs comme des impacts avec des astéroïdes ou des évènements volcaniques majeurs), la crise actuelle de la biodiversité est largement imputable aux activités anthropiques (Vitousek *et al.*, 1997; Chapin *et al.*, 2000). Les différents aspects de ces changements globaux induits par les activités humaines (réchauffement climatique, altération des flux géochimiques, changement d'utilisation des terres, introduction d'espèces envahissantes) contribuent simultanément, et parfois même en

synergie (Sala *et al.*, 2000), au déclin de la biodiversité. Le taux actuel d'extinction spécifique a été estimé 10 à 100 fois supérieur à celui pouvant être imputé aux processus naturels conduisant à la disparition de certaines espèces (Pimm *et al.*, 1995). Ce taux pourrait même être 10 000 fois supérieur si les espèces actuellement menacées venaient à s'éteindre. Plus généralement, la biodiversité, dans tous ses niveaux d'organisation, de la diversité génétique des populations à la diversité des paysages, est menacée à l'échelle planétaire (Chapin *et al.*, 2000).

Ces extinctions globales suscitent de nombreuses questions quant aux possibilités de conserver la diversité actuelle, mais également sur les impacts d'une telle crise sur le fonctionnement global de la biosphère, notamment: (i) dans quelle mesure cette crise de la biodiversité peut-elle profondément impacter le fonctionnement des écosystèmes ? (ii) toutes les espèces ont–elle la même importance au regard d'un processus écosystémique donné ? (iii) combien d'espèces sont nécessaires pour assurer les fonctions minimales des écosystèmes ?

1- Richesse spécifique et fonctionnement des écosystèmes :

Des effets souvent positifs du nombre d'espèces

Les facteurs abiotiques (tels que le climat, les caractéristiques des sols) influencent à la fois la diversité (le nombre d'espèces, leur abondance relative) d'une communauté et les processus écosystémiques (Chapin *et al.*, 2000; Chapin *et al.*, 2002; Lavorel *et al.*, 2002). Diversité et processus écosystémiques peuvent donc co-varier, sans relation causale, s'ils sont, par exemple, contôlés par les mêmes ressources (Wardle, 2001). De tels effets confondants des facteurs abiotiques limitent notre capacité à appréhender le rôle de la diversité spécifique sur le fonctionnement des écosystèmes en milieu naturel. La manipulation expérimentale de la diversité spécifique s'est alors révélée nécessaire pour comprendre les bases d'une relation biodiversité - fonctionnement.

Au cours des 20 dernières années, cette question de la relation biodiversité - fonctionnement a stimulé la mise en place de plusieurs centaines d'expérimentations (Balvanera *et al.*, 2006; Cardinale *et al.*, 2006). Ces expérimentations ont le plus généralement

consisté en une étude comparative d'assemblages d'espèces, au sein d'un niveau trophique donné, artificiellement créés en laboratoire ou sur le terrain, et dont la richesse spécifique (correspondant au nombre d'espèces) variait. La plupart de ces études ont cherché à déterminer s'il existait ou non une relation entre le nombre d'espèces, par exemple de plantes (Tilman *et al.*, 1997a; Tilman *et al.*, 1997b; Hector *et al.*, 1999), de micro-organismes décomposeurs (Tiunov & Scheu, 2004; Bell *et al.*, 2005), d'invertébrés benthiques (Covich *et al.*, 1999), etc. sur les processus que ces espèces influencent. La variété des processus mesurés peut se regrouper en trois classes (Reiss *et al.*, 2010): production de biomasse, consommation de ressource, et respiration. Ces propriétés écosystémiques peuvent être mesurées comme la « taille » d'un compartiment trophique donné (valeurs de biomasse, abondance d'individus, stock de carbone…) ou le taux d'un processus (productivité primaire, vitesse de décomposition …).

Globalement, ces études expérimentales ont mis en évidence un effet souvent positif du nombre d'espèces sur les processus écosystémiques (Balvanera *et al.*, 2006) (Fig. 1). Cependant, l'interprétation mécaniste (voir Encadré 1) des relations empiriques entre richesse spécifique et processus écosystémiques, ainsi que la forme de cette relation (différente en fonction du type d'organismes, de processus ou d'écosystème considérés) ont suscité de vifs débats au sein de la communauté scientifique (Aarssen, 1997; Huston, 1997). A l'issue de ces débats, un cadre conceptuel fort a émergé (Loreau *et al.*, 2001; Hooper *et al.*, 2005) et les avancées dans ce champ de recherche ont été présentées comme un nouveau paradigme de l'écologie (Naeem *et al.*, 2002; Loreau, 2010).

Un lien ni simple, ni universel

Alors que certaines expérimentations reportaient une relation linéaire positive entre richesse spécifique et processus écosystémiques (Hector 1999), d'autres études mettaient en évidence une saturation à un certain niveau de richesse spécifique, parfois relativement bas (Naeem, 1998; Waide *et al.*, 1999). Cette saturation serait l'indication d'une certaine redondance entre les espèces, suggérant que de nombreuses espèces peuvent avoir le même rôle fonctionnel (Walker, 1992). Dans d'autres cas, la relation entre le nombre d'espèces et le processus étudié est apparue idiosyncrasique, c'est-à-dire non prévisible (Emmerson *et al.*,

2001). Ce type de relation est particulièrement récurrent dans les études qui considèrent les effets de la diversité « after-life » des producteurs primaires, c'est-à-dire le rôle de la diversité des litières issues des plantes sur la décomposition ou le recyclage des nutriments (Wardle *et al.*, 1997; Gartner & Cardon, 2004; Hättenschwiler *et al.*, 2005). Une relation idiosyncrasique cependant ne reflète pas nécessairement une absence d'effet de la diversité. Quand les processus sont comparés entre les effets observés du mélange, et les effets attendus sans interaction entre les espèces (donc basés sur les espèces en monocultures), il apparaît généralement des effets non-additifs des mélanges (Zak *et al.*, 2003; Dijkstra *et al.*, 2005). Dans le cas des effets de la diversité des litières, ces effets-non additifs ont été mis en évidence dans plus de la moitié des études, et sont le plus souvent synergiques (Gartner & Cardon, 2004).

Encadré 1: Les mécanismes d'une relation entre diversité et processus écosystémiques :

L'interprétation des relations empiriques entre diversité et processus écosystémiques a été sujette à controverse, à cause de la difficulté d'interprétation des mécanismes sous-jacents, notamment à cause des effets confondants liés à l'identité des espèces (Grime, 1997). Un effet positif du nombre d'espèces peut en effet intervenir de façon probabiliste : plus le nombre d'espèces est élevé, et plus la probabilité d'inclure une espèce qui a un fort effet positif sur le processus étudié augmente (Aarssen, 1997; Huston, 1997). Cet effet a été considéré comme un artéfact expérimental (« sampling effect ») ou résultant des processus naturels d'assemblages des communautés (« effet de sélection ») (Loreau *et al.*, 2001). Toutefois, il existe des effets de complémentarité entre les espèces qui englobent deux mécanismes distincts : la différenciation de niches écologiques spatiales ou temporelles, et la facilitation (Loreau *et al.*, 2001). La différenciation des niches devrait favoriser une complémentarité de l'utilisation des ressources. Les espèces exploitent des ressources différentes, et une plus grande diversité d'espèces permettrait une meilleure exploitation globale des ressources, et donc un meilleur fonctionnement de la communauté (Cardinale *et al.*, 2007). La facilitation, quant à elle, désigne toute interaction positive entre organismes bénéficiant à au moins un des organismes en interaction, sans nuire à aucun autre (Bruno *et al.*, 2003). Par exemple, dans le cas de la décomposition des litières, les activités de consommation de la litière d'une espèce de champignons peuvent être augmentées par les activités de consommation d'une autre espèce de micro-organisme décomposeur (Tiunov & Scheu, 2005). Ces différents mécanismes ne sont pas exclusifs et peuvent opérer simultanément (Hooper *et al.*, 2005).

Concernant les effets de la diversité des litières sur le processus de décomposition ou sur les cycles des nutriments, il a été proposé plusieurs mécanismes (par exemple des transferts de composés chimiques, un meilleur équilibre nutritionnel pour les organismes décomposeurs) (Hattenschwiler *et al.*, 2005; Gessner *et al.*, 2010). L'identification et la caractérisation des mécanismes générant des effets non-additifs dans les mélanges de litières est l'un des points centraux présentés au cours de cette thèse.

Malgré un grand nombre d'expérimentations, il existe un fort déséquilibre dans la représentativité du type d'organismes, de processus ou d'écosystèmes considérés. En effet, la plupart de ces expérimentations ont été centrées sur les changements de productivité primaire en fonction de la diversité d'espèces prairiales. Dans une méta-analyse reportant 446 études (Fig. 1), 246 d'entre elles concernaient des écosystèmes prairiaux, et 242 des mesures de productivité primaire (Balvanera *et al.*, 2006). Ainsi, le rôle de la biodiversité pour la décomposition et le recyclage des nutriments a été comparativement moins étudié (Gessner *et al.*, 2010).

Bien que l'analyse des relations entre le nombre d'espèces (au sein d'un compartiment trophique donné) et les processus ait confirmé dans un assez grand nombre de cas un effet positif de la diversité, le pouvoir explicatif du nombre d'espèce est assez faible (Hooper *et al.*, 2005). Le plus souvent, l'effet de l'identité des espèces, ou de la combinaison particulière de certaines espèces, apparaît prédominant. Pour prendre en compte ces effets liés à l'identité des espèces (qui peuvent être additifs ou non-additifs), l'attention s'est rapidement portée vers les composantes de la diversité qui sont fonctionnellement impliquées dans cette relation, et ainsi vers l'identification de traits fonctionnels clés (voir Encadré 2).

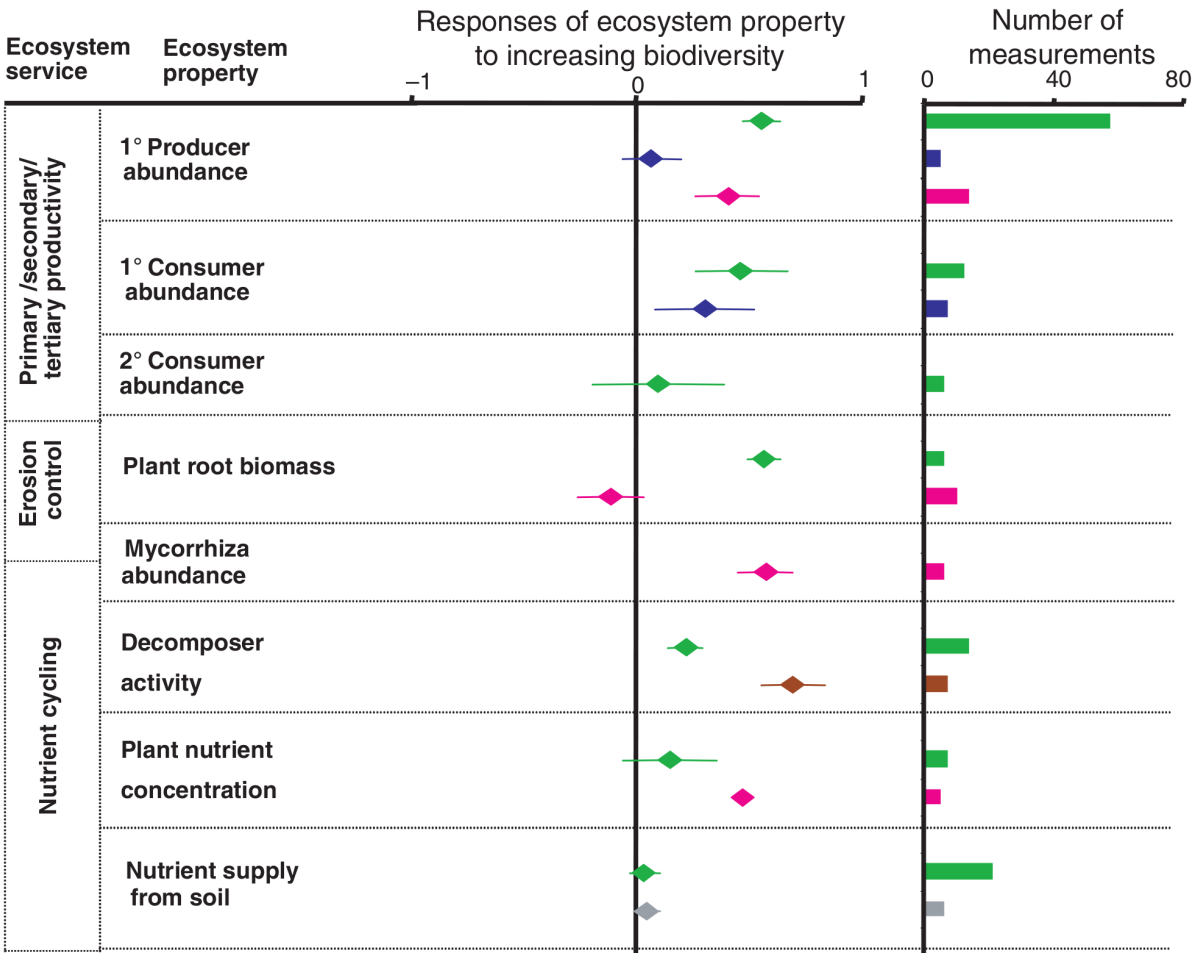

Figure 1: Magnitude et direction des effets de biodiversité et le nombre de mesures disponibles pour différentes fonctions écosystémiques. Les barres colorées représentent différents niveaux trophiques ; en vert : les producteurs primaires ; en bleu : les consommateurs primaires ; en rose : les mycorhizes ; en marron : les décomposeurs ; en gris : différents niveaux trophiques manipulés simultanément (d'après Balvanera *et al.*, 2006).

2- Vers une meilleure intégration de la diversité fonctionnelle :

La richesse spécifique ne reflète qu'une partie de l'organisation biologique. Pour approfondir l'analyse des mécanismes impliqués dans la relation biodiversité-fonctionnement, les recherches se sont rapidement axées sur ce que les espèces font, plutôt que de considérer seulement le nombre d'espèces. En effet, la diversité a des conséquences fonctionnelles parce que le nombre et le genre d'espèces présentes déterminent les traits des organismes qui influencent les processus écosystémiques (Chapin *et al.* 2000 ; voir Encadré 2).

Quand les espèces sont regroupées suivant des groupes ou des types fonctionnels (voir Encadré 2), la richesse en groupe fonctionnels (c.-à-d. leur nombre) peut avoir un pouvoir explicatif plus fort que le nombre d'espèces (Hooper & Vitousek, 1997; Tilman *et al.*, 1997a). Cependant, cette classification fonctionnelle reste arbitraire, et s'avère limitée pour décrire la diversité fonctionnelle (Wright *et al.*, 2006) pour plusieurs raisons : i) les résultats peuvent dépendre de la manière de grouper les espèces, ii) la formation de groupes entraîne une perte d'informations en ce qui concerne les variables quantitatives et iii) l'approche ne prend pas en compte l'abondance relative des espèces (Mason *et al.*, 2005).

Par conséquent, la définition de métriques continues de diversité fonctionnelle est en plein essor. Leur formulation mathématique s'avère cependant complexe (Petchey & Gaston, 2006). Les mesures proposées pour quantifier le degré de différentiation fonctionnelle des espèces sont basées sur la distance entre les espèces, chaque espèce étant considérée comme un point dans un espace à n dimensions, n étant le nombre de caractères (trait fonctionnels) mesurés sur l'ensemble des espèces (Botta-Dukat, 2005; Petchey & Gaston, 2007). Cependant, plutôt que d'utiliser un seul indice, Mason et collaborateurs (2005) suggèrent d'en utiliser plusieurs, afin de prendre en compte les différentes facettes de la diversité fonctionnelle, à savoir la richesse, l'équitabilité et la divergence fonctionnelle. Actuellement, il existe encore peu d'études utilisant ces mesures continues de diversité fonctionnelle.

Encadré 2: Approche fonctionnelle du vivant et des effets « after-life » des producteurs primaires

L'approche fonctionnelle du vivant repose sur l'idée qu'une espèce peut être décrite par un ensemble de caractéristiques, ou traits, qui reflètent leur écologie, leur fonctionnement (croissance, reproduction), dans un milieu donné. La classification fonctionnelle du vivant s'est d'abord développée pour comprendre les règles d'assemblages des espèces au sein des communautés. Avec l'émergence de la question du rôle fonctionnel de la diversité, une synthèse de ces deux approches a été combinée : les traits fonctionnels des espèces peuvent être les révélateurs de la réponse des espèces aux variations des facteurs de l'environnement et/ou les médiateurs des effets de leur fonctionnement sur les processus écosystémiques (Lavorel & Garnier, 2002).

Trait fonctionnel : composante du phénotype des organismes qui reflète leurs réponses aux variations des facteurs du milieu (trait de réponse) et/ou leurs effets sur les processus écosystémiques (trait d'effet). Il s'agit de caractéristiques morphologiques, physiologiques, ou phénologiques mesurables à l'échelle de l'individu (de la cellule à l'organisme entier) sans référence à aucun autre niveau d'organisation (Violle *et al.*, 2007) et qui reflète indirectement ou directement une fonction de l'organisme (croissance, reproduction…).

Groupe ou type fonctionnel : regroupement de plusieurs espèces ayant les mêmes traits de réponse et/ou les mêmes traits d'effets

Les espèces végétales peuvent largement affecter le fonctionnement souterrain, notamment à travers les apports de matière organique qu'elles fournissent au sol (Eviner & Chapin, 2003b; Wardle *et al.*, 2004). La qualité des litières foliaires (c.-à.d. les caractéristiques physiques ou chimiques des litières) varie en fonction des espèces végétales dont elles dérivent (Perez-Harguindeguy *et al.*, 2000; Hättenschwiler *et al.*, 2008). Ces variations de qualité se traduisent par une décomposabilité différentielle en fonction des espèces avec d'importantes conséquences pour le fonctionnement du sol (Swift *et al.*, 1979 ; Cadisch & Giller, 1997). Récemment, une étude a mis évidence que les apports de bois mort variaient aussi en termes de qualité suivant les espèces d'arbres dont ils sont issus, se traduisant ainsi par des vitesses de décomposition différentes (Van Geffen *et al.*, 2010). On peut ainsi raisonnablement appliquer le terme de trait fonctionnel (comme trait d'effet) à toute caractéristiques physiques ou chimiques des parties-non vivantes issues des végétaux (litière foliaire et bois), identifiables et attribuables à l'espèce dont elles sont issues, et, ayant un effet sur les processus écosystémiques.

II. La décomposition, un processus clé du fonctionnement des écosystèmes

Dans les écosystèmes forestiers, moins de 10 % de la productivité primaire nette aérienne est utilisée pour l'organisation des réseaux trophiques aériens, des herbivores aux carnivores (Chapin *et al.*, 2002). Ainsi, plus de 90% de cette productivité retourne au sol, sous forme de matière organique morte (litières foliaires, bois, fruits …), fournissant à la fois nourriture et habitat pour l'ensemble des organismes souterrains (Takeda & Abe, 2001; Chapin *et al.*, 2002). Les litières foliaires, comme apport de matière organique morte majoritaire dans les écosystèmes forestiers (avec la rhizodéposition), constituent une ressource primordiale d'énergie et de nutriments pour les organismes décomposeurs.

La décomposition de la matière organique est l'ensemble des transformations physiques et chimiques, réalisées par les actions conjointes des organismes et de facteurs abiotiques (Swift *et al.*, 1979). Cet ensemble de transformations est graduel et comparable à un système de poupées russes (Eijsackers & Zehnder, 1990) : à chaque étape, la matière organique subit la même séquence de processus (lessivage, altération chimique liée au catabolisme des organismes, et réduction de la taille des particules) produisant ainsi de « nouvelles » ressources pour les séquences de transformations suivantes. La décomposition aboutit ultimement à (i) la minéralisation des éléments, correspondant à la conversion de la forme organique d'un élément en sa forme inorganique (CO_2, nutriments minéraux) et à (ii) la formation de la matière organique du sol à travers l'humification (Swift *et al.*, 1979). La formation de l'humus résulte de la transformation de la matière organique en composés organiques complexes. Ces derniers étant difficilement utilisables par les micro-organismes et ne pouvant être lessivés, l'humus a généralement un long temps de résidence dans les sols.

La décomposition, à travers la minéralisation et la formation de la matière organique des sols, détermine dans une large mesure la structure des communautés végétales et le fonctionnement des écosystèmes (Swift *et al.*, 1979; Xiong & Nilsson, 1999). Il s'agit du seul processus écosystémique permettant un recyclage massif des nutriments, les rendant de nouveau disponibles pour la nutrition des plantes et des micro-organismes (Chapin *et al.*,

2002). À travers le relargage du carbone, sous forme de CO_2 issu de la respiration des décomposeurs, la décomposition joue également un rôle majeur sur le cycle global du carbone (Raich & Schlesinger, 1992). De surcroit, l'humification joue un rôle important sur la séquestration à long terme du carbone, ainsi que sur la fertilité des sols, mais ces effets à long terme sont encore mal compris (Berg & Mcclaugherty, 2003).

1- Un processus multitrophique :

Une partie du processus de décomposition résulte du lessivage, c'est-à-dire de l'entraînement physique par l'eau des ions minéraux et des petites molécules organiques. Les composés lessivés peuvent avoir des effets importants sur la dégradation ultérieure de la ressource organique en stimulant les activités microbiennes (à travers le lessivage de nutriments ou de petites molécules carbonées simples et riches en énergie) ou en les inhibant (à travers le lessivage de certains composés phénoliques) (Eijsackers & Zehnder, 1990). Bien que les pertes par lessivage ne soient pas négligeables (particulièrement dans les écosystèmes où les précipitations sont fortes) (Wieder *et al.*, 2009), la décomposition est un processus largement biologique, conduit par une communauté incroyablement diverse de saprophages (c.-à-d. de consommateurs de matière organique morte). Ce type de régime alimentaire est présent dans la majorité des groupes d'organismes du sol, généralement classifiés en fonction de leur taille. Ainsi, les saprophages sont distingués en deux grands groupes : les détritivores (animaux consommateurs de matière organique morte) et les micro-organismes décomposeurs (champignons et bactéries). La décomposition se réalise au travers d'une cascade d'évènements trophiques : elle dépend des interactions entre ces deux groupes de saprophages, mais aussi de leur régulation par les forces de prédation.

Les détritivores

Les détritivores incluent de nombreux groupes d'organismes, distingués en deux groupes en fonction de leur taille : la mésofaune (acariens, collemboles, enchytreides …) et la macrofaune (isopodes, millipèdes, vers de terres…) (Bardgett, 2005). Ils ont un impact direct sur la décomposition et la minéralisation de la ressource organique à travers leur assimilation de la matière (Petersen & Luxton, 1982; Verhoef & Brussaard, 1990). Les taux d'assimilation sont cependant très variables selon les espèces (David & Handa, 2010), mais relativement faibles, n'excédant que rarement 20% (Wolters, 2000). Par exemple, en forêt méditerranéenne, si le diplopode *Glomeris marginata* consomme 43% des apports annuels de litière de chêne vert (David & Gillon, 2002), il assimile seulement 6% de la matière, le reste étant rejeté sous forme de boulettes fécales. Bien que significatif, le rôle direct des détritivores sur la minéralisation de la matière organique est limité, représentant environ 10% de la respiration totale du sol (Seastedt, 1984).

La faune saprophage du sol joue un rôle indirect prépondérant sur la décomposition et influence largement le devenir de la matière organique (Scheu & Wolters, 1991). En transformant une partie de la ressource organique en boulettes fécales, la faune produit de nouvelles ressources, différentes en termes de structure et de chimie pour les autres organismes. Les boulettes fécales fournissent un environnement favorable pour la croissance microbienne (plus particulièrement bactérienne) conduisant généralement à une augmentation des taux de décomposition et du recyclage des nutriments (Zimmer & Topp, 2002). En brisant de larges morceaux de matière organique, les détritivores modifient également la structure physique de la litière. La fragmentation permet de créer des surfaces nouvelles pour la colonisation microbienne (en modifiant le rapport volume/surface de la matière organique), et augmente ainsi les taux de décomposition (Wolters, 2000). Les activités de bioturbation des organismes ingénieurs du sol (en mélangeant la matière organique en décomposition à la fraction minérale du sol) peuvent augmenter la disponibilité en nutriments pour les micro-organismes colonisant la matière organique. Enfin, les détritivores influencent la structure et la composition des communautés de micro-organismes.

Champignons et bactéries

Les bactéries et les champignons, à travers la libération d'exo-enzymes, sont les principaux acteurs de l'altération chimique du substrat organique. Ensemble, bactéries et champignons sont les organismes les plus abondants dans le sol. Par exemple, il peut y avoir 250 kg. ha^{-1} d'hyphe sur une surface de 5 cm de sol prairial (équivalent à 3km d'hyphe par gramme de sol), contenant 8 kg. ha^{-1} d'azote et 2 kg. ha^{-1} de phosphore (Bardgett, 2005). Le nombre de bactéries a quant à lui été estimé à plus d'un milliard par gramme de sol forestier (Horner-Devine *et al.*, 2004). A un tel niveau d'abondance, la quantité d'éléments chimiques présents dans les micro-organismes du sol est comparable à celle présentes dans les plantes terrestres, illustrant l'importance de ces organismes dans les processus biogéochimiques du sol (Coleman & Whitman, 2005).

Les champignons sont mieux équipés que les bactéries pour dégrader les molécules complexes (comme la lignine). Ils produisent généralement des hyphes filamenteux qui leur permettent de pénétrer et d'explorer les micro-habitats du sol, tandis que les bactéries sont plus limitées dans leur exploration, malgré une certaine capacité de dispersion. La capacité des champignons à exploiter de nouvelles ressources, et à transporter des nutriments à travers leur réseau mycélien, leur confère un avantage par rapport aux bactéries, particulièrement quand les nutriments sont limitants (Boddy, 1999).

L'altération chimique de la matière organique est ainsi largement conduite par les enzymes bactériennes et fongiques, et le processus de décomposition peut être représenté comme une succession de boucles au cours desquelles de fortes interactions s'établissent entre la composition chimique du substrat et la composition des communautés microbiennes (Moorhead & Sinsabaugh, 2006). La vitesse de décomposition suit généralement une courbe exponentielle, où trois phases d'altération chimique peuvent être identifiées (Couteaux *et al.*, 1995, Chapin *et al.,* 2002) (Cf. Figure 2). Moorhead et Sinsabaugh (2006) proposent de coupler ces changements de composition chimique du substrat aux activités de trois guildes écologiques de micro-organismes (différentes en termes de capacités enzymatiques) :

Phase 1 : lors de la phase initiale de lessivage très rapide, la guilde des micro-organismes opportunistes colonise rapidement la matière organique fraichement déposée et assimile les composés solubles sans l'aide d'enzymes extracellulaires.

Phase 2 : quand les substrats solubles disparaissent, les opportunistes sont remplacés par la guilde des décomposeurs capables de dégrader les hydrates de carbone non lignifiés (cellulose et hemicellulose).

Phase 3 : la décomposition ralentit ensuite fortement, en lien avec la dégradation lente des composés récalcitrants par la guilde des « mineurs » (Moorhead & Sinsabaugh, 2006). Les micro-organismes de cette guilde ont des taux de croissance faibles en lien avec le faible retour sur investissement des enzymes qui oxydent la lignine.

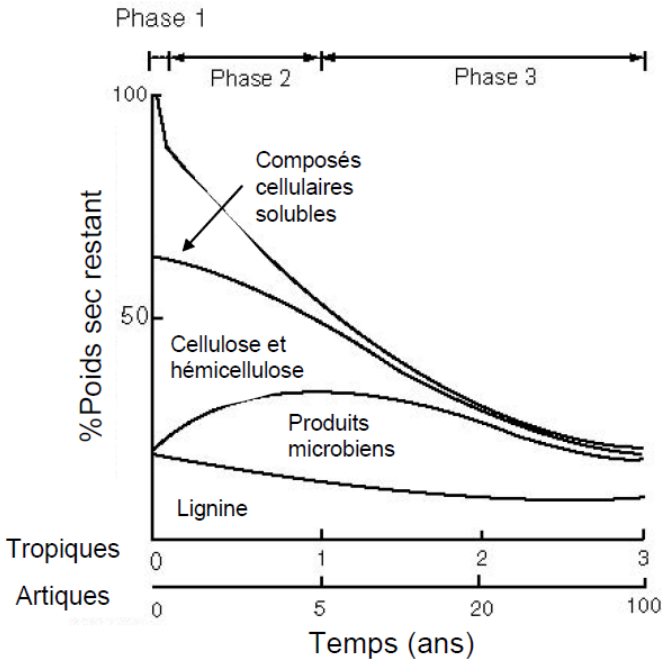

Figure 2: Représentation des trois phases majeures de la décomposition des litières et des échelles temporelles pour les biomes tropicaux et arctique. Le lessivage domine pendant les premières phases de décomposition. La qualité de la litière change au cours de la décomposition car les composés cellulaires solubles se décomposent beaucoup plus rapidement que les composants résistants des litières tels que la lignine et les produits microbiens (d'après Chapin *et al.*, 2002).

Importance de la structure du réseau trophique souterrain

Les saprophages sont intégrés dans un réseau trophique souterrain vaste, complexe et extrêmement diversifié. Les taux de décomposition dépendent de toute une cascade d'interactions trophiques au sein de ce réseau. La structure des communautés de saprophages et leur fonctionnement sont non seulement régulés en amont par les ressources organiques issues des producteurs primaires (forces ascendantes ou « bottom-up »), mais aussi par des forces descendantes (ou « top down ») liées à la prédation des décomposeurs. Plusieurs études expérimentales ont ainsi mis en évidence que la structure globale du réseau trophique peut affecter à la fois les taux de décomposition et les cycles des nutriments (Milton & Kaspari, 2007). Par exemple, Santos et Whitford (1981) mettent en évidence que la réduction des mites prédatrices conduit à l'abondance de leurs proies, des nématodes se nourrissant de bactéries, et ainsi favorise la croissance microbienne et les taux de décomposition.

2- La qualité de la ressource organique issue des producteurs primaires régule fortement la décomposition :

L'apport de litière dans le sol est une source majeure de matière organique, constituant la base vitale d'une très grande diversité d'organismes édaphiques hétérotrophes. Les plantes contiennent toutes des protéines, de l'amidon, de la cellulose, de l'hémicellulose, des lipides et des polyphénols, mais les proportions relatives de ces composés varient en fonction des individus, des espèces et du stade de développement. L'ensemble des variations de ces composés, ainsi que la structure physique de la feuille, déterminent l'accessibilité de ces éléments chimiques essentiels pour les organismes du sol. Ainsi, la quantité et la qualité de la litière conditionnent fortement la structure et le fonctionnement des communautés hétérotrophes du sol (Cadisch & Giller, 1997). Parce qu'il s'agit d'un processus davantage contrôlé par des organismes que par des facteurs physiques, la décomposition est façonnée par les forces évolutives qui influent sur la croissance, la survie et la reproduction des organismes saprophages (Chapin *et al.*, 2002). L'environnement

physico-chimique (climat, nature du sol) ainsi que la structure du réseau trophique souterrain (« top-down effect ») contrôlent donc aussi largement les activités des décomposeurs.

Ainsi, les multiples interactions entre l'environnement physico-chimique, la quantité et la qualité de la matière organique, ainsi que la nature des communautés de décomposeurs (Swift *et al.*, 1979; Aerts, 1997) influencent fortement les taux de décomposition des litières, et ce à différentes échelles spatiales et temporelles. Lavelle et collaborateurs (1993) ont proposé de hiérarchiser l'importance de ces facteurs en fonction de l'échelle spatiale considérée. A large échelle, il a été montré que l'évapotranspiration actuelle (AET, un indice qui intègre à la fois la température et l'humidité) explique la variation des taux de décomposition entre les différents biomes (Aerts, 1997; Gholz *et al.*, 2000). A une échelle plus locale, dans des conditions climatiques similaires, les traits des litières (correspondant à la qualité, Cf. Encadré 1) exercent un contrôle prédominant sur les taux de décomposition (Couteaux *et al.*, 1995; Cornelissen, 1996; Aerts, 1997; Berg, 2000). De récentes études remettent cependant en cause cette hiérarchisation (Cornwell *et al.*, 2008; Zhang *et al.*, 2008) en montrant que les traits des plantes (Cornwell *et al.*, 2008) ou des litières (Zhang *et al.*, 2008) expliquent plus largement la variation des taux décomposition à l'échelle globale que les forces abiotiques. Par exemple, Zhang et collaborateurs (2008) ont mis en évidence, à partir des données provenant de 110 sites expérimentaux, issus de tous les biomes terrestres, que 70 % de la variation des taux de décomposition peut être prédite uniquement par le contenu total en nutriment (N, P, K, Ca, Mg) et le rapport C:N des litières (87% de la variation était prédite en incluant les variables climatiques).

L'influence de la qualité des litières sur la décomposition a été intensivement étudiée, principalement à travers des approches corrélatives (Cadisch & Giller, 1997). Les indices de qualité les plus souvent retenus comme facteurs explicatifs des taux de décomposition sont le rapport C:N, la teneur en lignine, ou le rapport lignine:N (Melillo *et al.*, 1982; Moore *et al.*, 1999), et peuvent être utilisés dans les modèles biogéochimiques globaux (Moorhead *et al.*, 1999; Adair *et al.*, 2008). Cependant, il n'existe pas de paramètre universel de qualité des litières permettant de prédire la décomposition au sein de chaque biome. D'autres traits, comme le ratio C:P (Wieder *et al.*, 2009), les polyphénols (Loranger *et al.*, 2002; Coq *et al.*,

2010), les composés carbonés solubles (Allison & Vitousek, 2004), et même des traits physiques comme la dureté des feuilles (Perez-Harguindeguy *et al.*, 2000), peuvent aussi être corrélés au taux de décomposition.

Plus que des approches corrélatives, une compréhension mécaniste des contraintes énergétiques et nutritionnelle (basée sur des approches expérimentales) est nécessaire pour comprendre le contrôle de la qualité de la ressource organique sur le fonctionnement des communautés de décomposeurs.

III. Limitation en ressources et approches stœchiométrique des interactions plantes- décomposeurs

1- Pourquoi et comment étudier les limitations nutritives des processus ?

Les éléments nutritifs comprennent jusqu'à 25 éléments chimiques essentiels pour la croissance des êtres vivants (Sterner & Elser, 2002). Ce nombre peut varier dans une certaine mesure, car certains éléments ne sont nécessaires que pour certains groupes d'organismes ou dans des circonstances spécifiques. Toutefois, une partie de ces éléments peuvent être en quantité insuffisante dans le milieu ou dans la ressource alimentaire (et/ou difficilement accessibles) relativement à la demande de l'organisme, devenant ainsi limitant pour sa croissance et/ou sa survie.

L'idée qu'un élément nutritif peut limiter un processus est apparue en 1840, quand Von Liebig suggère que la croissance d'une plante est limitée par l'élément nutritif à son plus bas niveau (relativement à la demande de la plante). Ce principe, énoncé dans le cadre de cultures végétales expérimentales, est couramment illustré à l'aide d'un tonneau (Cf. Figure 3) où les planches, chacune correspondant à une ressource indispensable, diffèrent par leur taille. La planche la plus courte indique l'élément qui est le plus limitant pour le processus, et ainsi de suite. À l'identique, la plante ne parvient pas à se développer de manière optimale tant que certaines ressources sont en quantités insuffisantes. La loi de Liebig est l'un des fondements de l'agriculture intensive depuis la moitié du XIXe siècle (Brock, 2002). Par extension de ce principe à l'écologie, la loi du minimum peut se définir pour tous les organismes (autotrophes et hétérotrophes) en considérant l'ensemble des facteurs qui leur sont limitant (eau, température, lumière, éléments chimiques…).

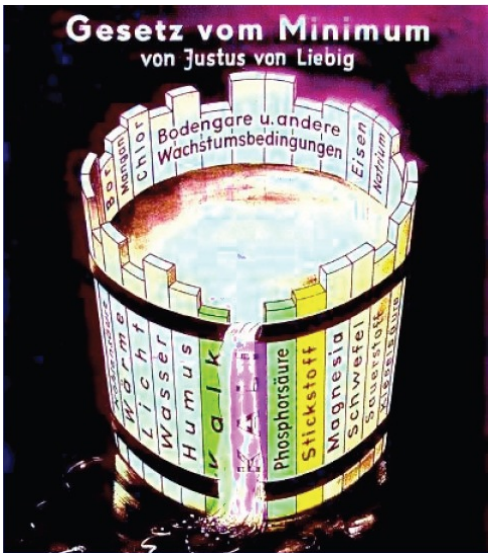

Figure 3: Représentation schématique de la loi de Liebig ou loi du minimum. En écologie, ce principe établit que la présence et le développement complet (jusqu'à la reproduction) d'une espèce dans un milieu donné sont conditionnés par le facteur qui (parmi ceux susceptibles d'être limitants), se trouve le plus proche d'un seuil - minimal ou maximal - de tolérance.

Plus qu'une science budgétaire qui viserait seulement à l'amélioration de la productivité d'un écosystème, l'étude des limitations nutritives des processus pose des questions fondamentales à différents niveaux d'organisation du vivant, des organismes aux écosystèmes. La disponibilité en nutriments essentiels façonne le fonctionnement, la composition, la dynamique, la diversité et les interactions des populations végétales, animales et microbiennes, dans beaucoup d'écosystèmes, qu'ils soient terrestres, aquatiques ou marins (Vitousek, 2004). La compréhension des limitations nutritives est également cruciale pour comprendre et prédire la réponse des écosystèmes face aux changements globaux. Les cycles géochimiques globaux de l'azote sont altérés de façon substantielle par les activités humaines (Vitousek *et al.*, 1997; Galloway *et al.*, 2004), et plusieurs études mettent en évidence d'importantes répercussions pour le fonctionnement des écosystèmes ou la structure des communautés (Eviner & Chapin, 2003a). Toutefois, les impacts de tels changements peuvent varier très largement en fonction de l'écosystème considéré, en particulier suivant l'étendue ou le type de limitation nutritive (notamment en N et/ou P) (Townsend *et al.*, 2008). De même, les réponses des écosystèmes à l'augmentation en CO_2 dans l'atmosphère peuvent elles aussi dépendre de l'étendue et/ou du type de limitation nutritive (Schimel *et al.*, 1997; Oren *et al.*, 2001).

Les approches pour étudier les limitations nutritives à l'échelle d'un écosystème peuvent être indirectes, à travers l'étude de la variation d'un ou de plusieurs processus (productivité primaire, décomposition…) le long de gradient de fertilité des sols (Vitousek *et*

al., 2010). Cependant, ces approches indirectes sont très souvent insuffisantes, notamment à cause de la difficulté à quantifier les éléments réellement disponibles pour les organismes, ou, à séparer les différents facteurs de contrôle co-variant le long de gradients naturels (climat, statut en nutriments des sols, type de végétation). Selon Chapin et collaborateurs (1986) seules des preuves expérimentales, via l'addition de ressources, permettent réellement d'explorer l'étendue ou le type de limitations nutritives d'un écosystème. Un élément sera défini comme limitant quand son ajout entraîne la croissance des individus ou des populations, ou une augmentation de la vitesse du processus considéré. Cependant, la compréhension des limitations nutritives apparaît souvent plus complexes que la loi du minimum, notamment à cause de l'occurrence de multiples limitations en ressources. Une limitation multiple se produit quand l'addition simultanée de deux ressources (ou plus) favorise le processus considéré (Elser & Hamilton, 2007; Kaspari *et al.*, 2008; Vitousek *et al.*, 2010). Malgré la nécessité d'expérimentations factorielles pour comprendre les multiples contrôles exercés parmi la vingtaine d'élément chimiques qui construisent le vivant, la loi du minimum a largement conduit les écologistes à considérer uniquement l'élément nutritif le plus limitant de la vitesse d'un processus ou de la croissance des organismes (Kaspari *et al.*, 2008). Par conséquent, les expérimentations factorielles manipulant plus de deux éléments nutritifs, autres que l'azote et le phosphore, sont très rares (mais voir Scheu & Schaefer, 1998; Reed *et al.*, 2011).

Récemment, un travail théorique important (supporté par de nombreuses études expérimentales et comparatives) a permis d'intégrer l'étude des limitations nutritives dans une perspective très large, qui vise à comprendre les interactions trophiques et leurs conséquences écosystémiques à travers la disponibilité relative en éléments, c'est-à dire leur stœchiométrie (Sterner & Elser, 2002).

2- Les apports de la stœchiométrie écologique :

L'évolution d'un paradigme : la vie sous forme de ratio

Comme les interactions au sein de l'écosystème impliquent fondamentalement un ensemble de réactions chimiques, il est possible de concevoir les organismes comme des substances chimiques complexes qui interagissent, à la fois entre elles et avec le monde abiotique, selon un ensemble de réactions chimiques tout aussi complexes. Les réarrangements chimiques lors des interactions trophiques entre les organismes doivent suivre la loi fondamentale de conservation de la matière : la masse des éléments (C, N, P, Ca, K…) est conservée ; les éléments ne sont ni créés ni détruits, seulement transformés. Par conséquent, l'intégration de la composition chimique élémentaire des organismes dans l'étude des transferts d'énergie et de matière lors des interactions trophiques devrait permettre l'émergence de règles simples de fonctionnement des systèmes biologiques. Ce cadre de pensée a été popularisé par James J. Elser et collaborateurs, qui l'ont appelé « stœchiométrie écologique », puis « stœchiométrie biologique » (en y intégrant des aspects évolutifs). Au sens strict, la stœchiométrie établit la loi des proportions constantes des éléments dans les réactifs et les produits d'une réaction chimique donnée. En écologie, la stœchiométrie se réfère à la façon dont les éléments sont couplés au sein des organismes (leurs proportions relatives), au cours des processus cellulaires et physiologiques, et comment ce couplage affecte les cycles des nutriments et les transferts entre les niveaux trophiques. La théorie stœchiométrique repose essentiellement sur les différences de composition entre les organismes en interactions, ce qui peut à la fois influer sur l'efficacité et les conséquences écosystémiques (rétention de nutriments, biomasse) de leurs relations trophiques, mais également jouer un rôle dans les interactions non-trophiques de type compétition et mutualisme. La puissance de cette théorie est d'adopter une vision simplifiée du vivant, basée sur les ratios des éléments, le plus souvent le carbone, l'azote et le phosphore, pour prédire les processus (rétention de nutriments, biomasse…) à toutes les échelles, de la cellule à l'écosystème.

Redfield en 1958 a ouvert la voie de l'intégration de la stœchiométrie dans l'étude des systèmes marins. En effet, il montrait que le rapport C:N:P du phytoplancton marin d'une

valeur molaire de 106:16:1 était similaire à celui des océans. Depuis, les nombreux travaux intégrant explicitement la stœchiométrie (à travers des approches expérimentales, comparatives et théoriques) dans l'étude des écosystèmes marins sont au centre de la compréhension du fonctionnement de ces systèmes. La compréhension de la variation des ratios C:N:P au sein des organismes terrestres et de leurs conséquences écosystémiques est encore relativement limitée, mais, de plus en plus d'études intégrant la stœchiométrie dans l'étude des écosystèmes terrestres ont émergé ces dernières années. Par exemple, McGroddy et collaborateurs (2004a) ont compilé des valeurs des ratios C:N:P pour le feuillage et la litière des producteurs primaires à travers le monde, et mis en évidence de fortes variations des ratios stœchiométriques entre les biomes, avec notamment des ratios N:P particulièrement élevés en forêt tropicale. Cependant, les auteurs mettent en évidence que ces ratios N:P sont relativement contraints autour d'une valeur donnée au sein de chaque biome.

Outre la loi de la conservation de la matière, la théorie stœchiométrique repose sur un deuxième principe fondamental : l'homéostasie. L'homéostasie se définit comme la capacité des organismes à garder leur composition chimique élémentaire constante, indépendamment des changements de composition chimique de leur environnement et/ou des ressources organiques utilisées. La majorité des organismes hétérotrophes tendent généralement à être relativement homéostatiques. Généralement, il existe un fort déséquilibre à la base des réseaux trophiques, qui génère de fortes contraintes nutritionnelles et résulte en un recyclage différentiel des nutriments par les consommateurs (herbivores et décomposeurs). Par des mécanismes de pré-ingestion (sélection de nourriture) et post-ingestion (excrétion), ils sont capables de réguler leurs concentrations internes en éléments. Au contraire, les organismes autotrophes présentent très souvent des variations de leur stœchiométrie en réponse aux changements de composition du milieu ; ainsi, la stœchiométrie des organismes non-homéostatiques peut suivre celle des ressources, ou bien n'en dévier que légèrement.

Stœchiométrie et interactions producteurs primaires - décomposeurs

A travers des approches corrélatives, de nombreuses études mettent en évidence un fort contrôle stœchiométrique des taux de décomposition. Très souvent, le ratio C:N est utilisé pour prédire les taux de décomposition (Melillo *et al.*, 1982; Moore *et al.*, 1999; Berg & Laskowski, 2006) et, dans une moindre mesure, le ratio C :P (Aerts, 1997). Dans une méta-analyse regroupant les taux de décomposition de la matière organique morte issue d'une grande gamme de producteurs primaires, des macroalgues aux arbres, Enriquez et collaborateurs (1993) ont mis en évidence que les variations des ratios C:N et C:P étaient corrélées négativement à la décomposition. (Fig. 4)

Les producteurs primaires ont des ratios C:nutriments considérablement plus élevés que ceux des organismes décomposeurs (Hessen *et al.*, 2004; Cleveland & Liptzin, 2007). Dans les écosystèmes terrestres, ces différences sont en général exacerbées au moment de la sénescence des feuilles, par la résorption des nutriments (Hättenschwiler *et al.*, 2008). Selon la théorie de l'écologie stœchiométrique, les décomposeurs devraient être particulièrement limités en nutriments tandis qu'ils disposeraient d'un excès de C (énergie).

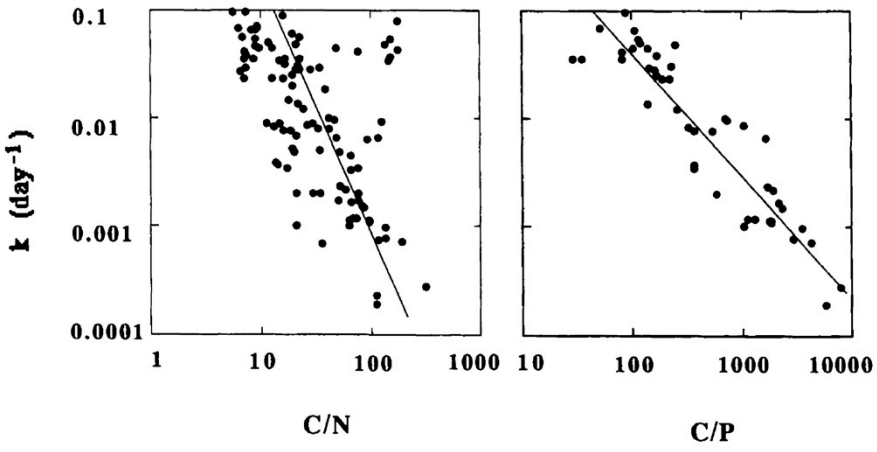

Figure 4: Relations entre taux de décomposition et ratios initiaux C:N et C:P des détritus (issues d'une grande gamme de producteurs primaires, des algues aux arbres) (d'après Enriquez *et al.*, 1993).

Dans un modèle théorique basé sur la stœchiométrie des interactions producteurs primaires et des décomposeurs, Daufresne et Loreau (2001) mettent en évidence qu'une limitation en nutriments et un excès d'énergie pour les décomposeurs signifie qu'ils sont en compétition directe avec les producteurs primaires pour les mêmes nutriments. Les auteurs soulèvent ainsi le problème de la coexistence stable et à long terme entre producteurs primaires et décomposeurs. À travers ce modèle qui intègre explicitement la stœchiométrie

de la ressource et celle des organismes décomposeurs, Daufresne et Loreau (2001) suggèrent plusieurs conditions sous lesquelles une coexistence stable entre producteurs primaires et décomposeurs est possible : i) si les nutriments limitant sont différents pour les producteurs primaires et les décomposeurs ou ii) si le contrôle des décomposeurs par les forces de prédation est plus important que le contrôle par la ressource ou encore iii) si les décomposeurs sont principalement limités par le C.

Ce type de modèle uniquement basé sur des simulations théoriques souligne l'importance d'évaluer le type de limitation en ressource des organismes décomposeurs, et de considérer simultanément les limitations potentielles en nutriments (principalement N et P) et en énergie (C).

3- L'importance de la forme biochimique du carbone pour les décomposeurs :

Le carbone issu de la ressource organique permet de fournir l'énergie nécessaire aux organismes décomposeurs à travers la rupture des liaisons carbone (Sterner & Elser, 2002). Cependant, le carbone total peut être un faible prédicteur de la quantité d'énergie réellement disponible parce que les différentes formes biochimiques du C imposent des degrés de récalcitrance différents, et donc des apports énergétiques très variables. Parmi les différentes formes de C, on peut distinguer (classées par ordre de récalcitrance et d'apport énergétique) : les composés carbonés solubles, les sucres, les hemicelluloses, la cellulose, les phénols (tanins condensés, la lignine)... Ainsi les teneurs de ces différentes formes biochimiques du C, plus que la quantité en C totale, peuvent imposer une limitation énergétique pour les décomposeurs.

Le rôle de la qualité du C comme facteur de contrôle des taux de décomposition est largement reconnu (Swift *et al.*, 1979) mais principalement à travers les teneurs en lignine (Berg & Laskowski, 2006). Il est très souvent considéré dans la littérature que les nutriments peuvent limiter la décomposition à court terme tandis qu'à long terme, la vitesse de décomposition est contrôlée par la proportion de lignine restante (Couteaux *et al.*, 1995). Cependant, le rôle de la disponibilité des formes carbonées facilement accessibles a été très peu considéré dans les études portant sur la décomposition des litières. Ce manque de

considération est assez étonnant, d'autant qu'il a été montré que les activités des micro-organismes dépendent fortement de l'identité des formes carbonées (Waldrop & Firestone, 2004; Orwin *et al.*, 2006). Par ailleurs, de nombreuses études mettent en évidence que des ajouts de carbone labile (sucres, cellulose) dans les sols peuvent stimuler la dégradation de la matière organique récalcitrante du sol. Cet effet, couramment appelé « priming effect » a reçu une attention considérable ces dernières années pour la compréhension du cycle du carbone dans les sols (Fontaine *et al.*, 2003 ; Kuzyakov, 2010) mais n'a été que très rarement expérimenté sur des litières (Fontaine *et al.*, 2007; Chigineva *et al.*, 2009). Bien que le « priming effect » soit un phénomène souvent observé dans les sols, les mécanismes sous-jacents sont encore peu compris. Il a été supposé que le « priming effect » peut provenir d'un co-métabolisme : dans le cas où les organismes sont limités en énergie, l'ajout de C riche en énergie stimule les activités métaboliques des organismes, leur permettant ainsi de produire des enzymes énergétiquement plus coûteuse permettant de dégrader les composés carbonés récalcitrants (Kuzyakov *et al.*, 2000), notamment pour récupérer l'azote contenu dans cette matière récalcitrante (Craig Maclean *et al.*, 2005; Moorhead & Sinsabaugh, 2006). Fontaine et collaborateurs (2003) proposent que le « priming effect » soit contrôlé par l'intensité de la compétition entre les micro-organismes à stratégie r (à croissance rapide), qui utilisent des formes simples du C et riches en énergie, et les micro-organismes à stratégie K (à croissance lente), capables d'utiliser des formes carbonées récalcitrantes. Selon ce modèle, basé sur l'intensité compétition entre ces deux types de stratégies, une accélération d'utilisation de la matière organique récalcitrante, suite à l'addition de C riche en énergie, est possible seulement si une partie substantielle du C ajouté est utilisée par les micro-organismes à stratégie K.

IV. Biogéochimie des forêts tropicales humides : un contexte particulier

Les forêts tropicales humides[3] couvrent 6.8 x 10^6 km^2 des terres émergées et représentent un dixième de la surface boisée mondiale (Houghton *et al.*, 2000). À travers leurs vastes échanges d'énergie, d'eau, de carbone et de diazote avec l'atmosphère, elles jouent un rôle clé dans la régulation du climat et des cycles biogéochimiques à l'échelle planétaire (Bazzaz, 1998; Malhi *et al.*, 2002; Mayaux *et al.*, 2005). Ces forêts représentent 40% de la totalité du carbone stocké dans la végétation terrestre (Giardina *et al.*, 2004; Houghton, 2005).

Malgré leur importance pour la biogéochimie globale, la compréhension, la quantification et les prédictions des flux biogéochimiques dans ces forêts sont limitées en comparaison avec de nombreux autres biomes. Cette sous-représentation dans les études scientifiques peut s'expliquer en partie à cause des défis logistiques et de l'éloignement des sources de financement des activités scientifiques (Malhi *et al.*, 2008). De surcroit, la difficulté est accrue par la complexité biogéochimique des forêts tropicales. En effet, les effets combinés de la diversité végétale et de la variation des conditions abiotiques entre les différentes forêts favorisent une hétérogénéité biogéochimique exceptionnelle à de multiples échelles (Townsend *et al.*, 2008). Pourtant, l'amélioration de la compréhension des flux biogéochimiques, mais aussi de leur prévision en fonction des différents scénarii des changements globaux, sont cruciales dans ces forêts au vu de leur importance dans la biogéochimie globale de la planète.

[3] La forêt tropicale humide ou forêt équatoriale est un biome des zones intertropicales. Malhi & Wright (2004) définissent les forêts tropicales humides comme ayant en moyenne des précipitations annuelles de 2180 mm, entre trois et quatre mois de saison sèche, une température moyenne proche de 25.2 °C avec une amplitude de 3.2 °C.

1- Le paradoxe des forêts tropicales humide : une végétation luxuriante sur un désert nutritif :

L'observateur qui pénètre en forêt tropicale humide est généralement impressionné par l'exubérance de la végétation et les arbres gigantesques, dont on peine à voir la cime. Ces écosystèmes ont été très tôt décrits comme fortement productifs, et malgré de grandes variations dans les estimations (en fonction des méthodes de mesures ou des sites) , les différentes études révèlent une productivité primaire nette aérienne élevée (Del Grosso *et al.*, 2005). Récemment, à partir d'une grande base de données sur le cycle du carbone dans les écosystèmes terrestres, Luyssart et collaborateurs (2007) montraient une productivité primaire nette en forêt tropicale humide supérieure à celle de toutes les forêts des autres biomes (boréal, méditerranéen, tempéré, tempéré humide).

Paradoxalement, ces forêts croissent et se maintiennent le plus souvent sur des sols extrêmement vieux et appauvris en nutriments essentiels, comme le phosphore ou les cations majeurs (calcium, magnésium, potassium) (Walker & Syers, 1976; Vitousek, 1984; Crews *et al.*, 1995). Contrairement à l'azote d'origine atmosphérique (Cf encadré 3), le phosphore et les cations majeurs proviennent de l'érosion de la roche mère au moment de la formation des sols, quand celle-ci est encore affleurante. Pour la plupart des forêts tropicales humides, l'absence de perturbation majeure[4] depuis des millions d'années, combinée à de fortes précipitations qui lessivent ces éléments, ont contribué au cours des millénaires à un épuisement considérable, et irréversible, de ces nutriments dans les sols de plaines (Crews *et al.*, 1995).

[4] Des perturbations à large échelle comme des événements volcaniques, tectoniques ou de glaciations permettent un rajeunissement des sols, c'est-à-dire un retour vers un état initial d'affleurement de la roche mère. L'érosion de la roche permet de libérer à nouveau des éléments comme le P ou les cations majeurs. De fortes pentes favorisent un rajeunissement constant des sols dans les massifs montagneux. En conséquence les forêts tropicales humides d'altitude sont généralement plus riches en P que les forêts tropicales humides de plaine (Tanner et al., 1998).

Pour maintenir une productivité élevée, le cycle des éléments doit être particulièrement conservatif. En forêt tropicale, le cycle des nutriments est souvent caractérisé comme « fermé », ou efficient, comparativement à celui des forêts tempérées. Toutefois, une forte efficience[5] peut résulter de deux patrons distincts (Vitousek, 1984) :

i) l'utilisation des nutriments à l'intérieur des forêts tropicales peut être efficiente si une grande quantité de matière organique est fixée par unité de nutriments prélevés au sein des producteurs primaires. Autrement dit, les espèces végétales doivent développer des stratégies particulièrement efficaces de conservation des nutriments. Pour conserver ces ressources, les arbres peuvent fixer une plus grande proportion de carbone par unité de nutriments et/ou éviter de les perdre, à travers une forte résorption des nutriments à partir des parties sénescentes des arbres. Ces mécanismes de conservation ne concernent pas que le C, et ainsi, l'efficience d'utilisation des nutriments peut se caractériser par un rapport C/ nutriments élevé. Les mécanismes de résorption des nutriments avant la sénescence de feuilles ont pour conséquence des apports de litière particulièrement déséquilibrés en nutriments relativement au carbone (Hättenschwiler *et al.*, 2008).

ii) les cycles des nutriments peuvent être efficients si la plupart des nutriments recyclés à partir des arbres sont rapidement prélevés par les racines, les mycorhizes et les décomposeurs, et ainsi retenus à l'intérieur du système, de telle sorte que le lessivage des nutriments par les précipitations soit minimisé. L'efficience est dans ce cas caractérisée par une faible perte des nutriments à partir du système entier, malgré une large quantité des nutriments recyclés entre arbres et sols.

Ces deux patrons ne sont pas exclusifs, et l'ensemble des mécanismes évoqués agissent simultanément dans le contrôle des cycles des nutriments. Dans un cas comme dans l'autre, le maintien de la productivité en forêt tropicale dépend beaucoup plus du processus de reminéralisation des nutriments à travers la décomposition, que du stock des éléments dans les sols.

[5] L'efficience est un anglicisme issu de *efficiency* qui ne doit pas se confondre avec le terme d'efficacité. En écologie, l'efficience est définie pour un niveau trophique et correspond au rapport entre l'énergie fixée et l'énergie reçue.

Encadré 3: Les éléments nutritifs au cours de la formation des sols

Les éléments nutritifs sont distingués suivant leur source d'origine :

-l'atmosphère : une grande partie des cycles de l'azote et du carbone est sous forme gazeuse. L'azote entre dans les écosystèmes terrestres à travers la fixation biologique du N_2 et les dépôts atmosphériques.

-la roche : les éléments comme le P et les cations majeurs (Ca, Mg, K) sont d'importants constituants des minéraux et entrent dans les écosystèmes terrestres suite à la dissolution partielle ou complète de la roche mère (érosion chimique).

En se basant sur cette distinction, Walkers et Syers (1976) proposent une explication cohérente de l'évolution de la disponibilité en nutriments au cours du développement à long terme des sols. L'érosion chimique et physique de la roche mère est forte au début de la formation des sols. Les sols jeunes (dont la roche mère est affleurante) s'enrichissent rapidement en P et en cations majeurs, tandis qu'ils sont particulièrement pauvres en azote. A moins d'une perturbation pouvant rajeunir les sols, le stock de minéraux érodables diminue au cours du temps, et les éléments qui en sont dérivés (P, cations majeurs) sont perdus sans possibilité de remplacement.

Au contraire, la fixation biologique de l'azote atmosphérique et les dépôts atmosphériques augmentent la quantité et la disponibilité biologique de l'azote qui tend à s'accumuler dans l'écosystème au cours des temps géologiques. En plus de l'appauvrissement du stock de minéraux érodables, la diminution de la disponibilité en phosphore peut être exacerbée au cours du temps par son occlusion dans les minéraux secondaires, ou son piégeage dans la matière organique récalcitrante. Quand le phosphore complexe avec les oxydes et hydroxydes de fer et d'aluminium (particulièrement abondants dans les sols tropicaux), les minéraux secondaires ainsi formés peuvent mettre des centaines, voire des milliers d'années, avant d'être érodés et de devenir à nouveau disponibles pour les plantes et les micro-organismes (Vitousek *et al.*, 2010).

Ce modèle de formation des sols explique pourquoi les forêts tropicales (où les sols sont donc vieux, extrêmement lessivés et riches en minéraux secondaires) sont généralement limitées en P, alors que les forêts boréales et tempérées (où les sols ont subi d'importantes phases de rajeunissement au moment de la rétraction des glaciers lors des dernières périodes glaciaires) sont principalement limitées en N. Bien qu'il existe relativement peu de preuves expérimentales directes (via la fertilisation), de nombreuses preuves indirectes alimentent la théorie d'une limitation en P et d'une richesse en N dans les forêts tropicales humides (Fig. 5).

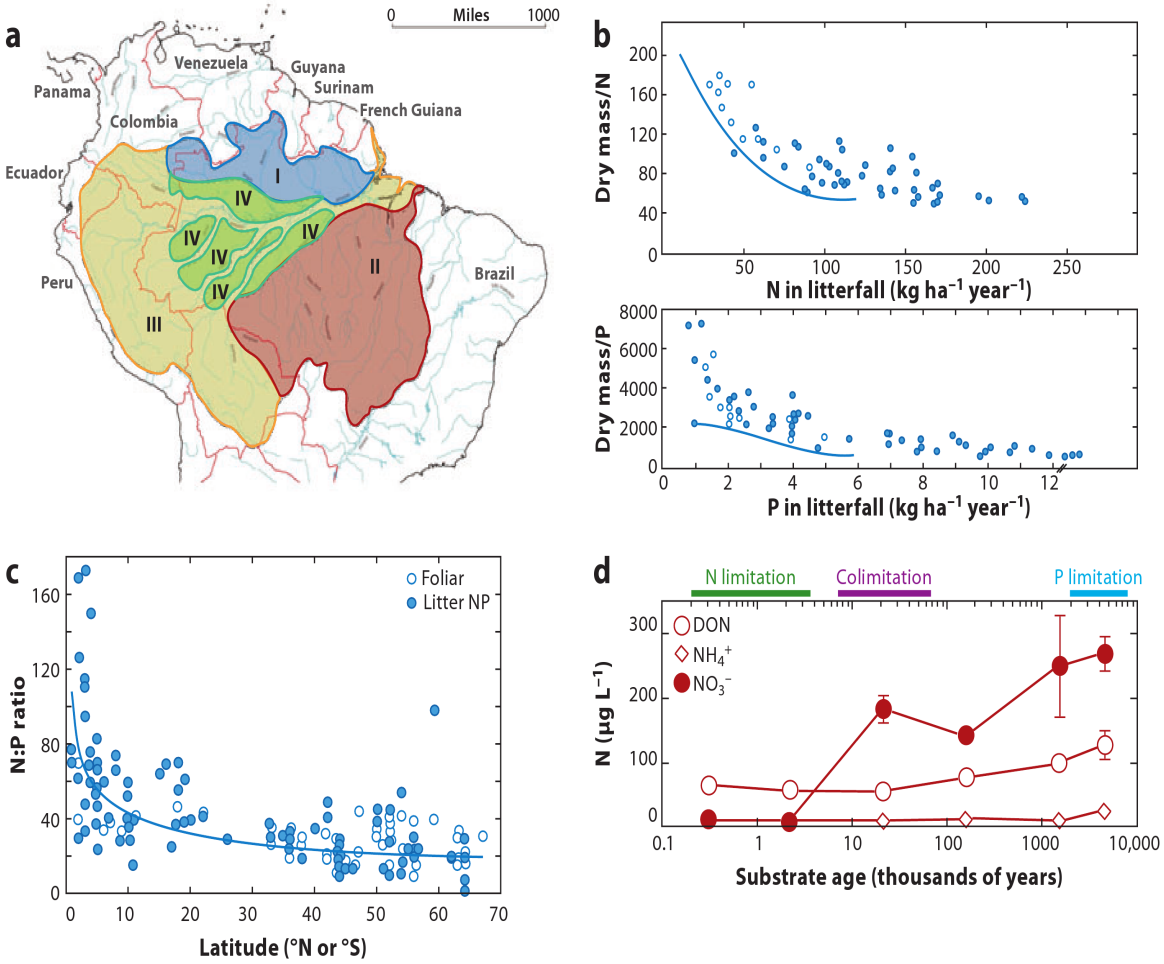

Figure 5: Illustration des différentes études permettant de souligner l'appauvrissement en P dans les sols tropicaux en comparaison d'une richesse en N (d'après Hedin *et al.*, 2009)

a) Les quantifications des concentrations en macronutriments dans les sols Amazoniens définissent 4 grandes sous régions écologiques : I : bouclier guyanais infertile et lessivés. II : bouclier brésilien : infertile et lessivé. III : Ouest Amazonien : ensemble hétérogène de sol plus fertiles et moins lessivés. IV : Amazonie Centrale : surface non fertile de sédiment originaire du bouclier guyanais et du bouclier brésilien.

b) A travers la quantification des éléments N et P dans les chutes de litières et l'estimation de la quantité annuelle de chutes de litières en forêt tropicale, (Vitousek, 1984) analyse l'efficience d'utilisation des nutriments de plantes (exprimée comme le rapport masse sèche : quantité de nutriments) en fonction des apports totaux annuels des nutriments dans la litière. La figure du haut représente une diminution de l'efficience de N en fonction des apports bruts de N dans les litières (points bleus) qui suit une tendance similaire à celle observée en forêt tempérée et boréale (courbe bleue). La figure du bas représente les mêmes analyses pour le P ; cependant pour un faible apport en P de la litière, on observe une meilleure efficience d'utilisation du P en forêt tropicale qu'en forêt tempérée.

c) Ratio molaire N : P des feuilles (cercles ouverts) et des litières (cercles bleus) dans des écosystèmes forestiers le long d'un gradient latitudinal. Le ratio N : P augmente quand la latitude diminue, en particulier pour les litières (Mcgroddy *et al.*, 2004a).

d) Perte en N le long d'un gradient d'âge des sols (4 millions d'années) qui représente un gradient de limitation en N et P (Vitousek & Farrington, 1997).

2- Hétérogénéité biogéochimique des forêts tropicales :

Le modèle d'évolution de la disponibilité en nutriments au cours du développement des sols proposé par Walker et Syers (1976) (Cf. Encadré 2) a conduit à la large acceptation d'une limitation en P dans les forêts tropicales humides. Cependant la grande variation des conditions biogéochimiques entre et au sein des forêts tropicales peut compliquer la généralisation d'une simple limitation en P.

Variation de la géochimie au sein du biome équatorial :

De récentes études (Bern *et al.*, 2005; Porder *et al.*, 2007) remettent partiellement en cause la vision statique de l'appauvrissement en éléments dérivés de la roche mère au cours des temps géologiques proposée par Walker et Syers (1976) (Cf. Encadré 2). En effet, ces auteurs ont mis en évidence qu'il existe des transports de matériaux issus de la roche mère des couches profondes vers la surface. L'intensité de ce type de transport varie largement en fonction des différentes régions tropicales (Porder *et al.*, 2007) conduisant à de grandes variations de la disponibilité de P dans les sols. De plus, Chadwick et collaborateurs (1999) ont mis en évidence des transports atmosphériques de poussières issues du désert du Sahara qui peuvent apporter des cations majeurs dans les zones tropicales sous influences maritimes.

Ainsi, il existe une forte variabilité à l'échelle régionale de combinaison d'âge des sols, de chimie de la roche mère initiale et de susceptibilité à l'érosion ou à la tectonique des plaques au sein du biome tropical (Townsend *et al.*, 2008; Quesada *et al.*, 2010). Ces différents facteurs peuvent par conséquent créer une large gamme de variation de concentrations en éléments nutritifs au sein des sols tropicaux, et les limitations nutritives peuvent être complexes.

Diversité fonctionnelle et hétérogénéité biogéochimique à l'échelle locale :

Les forêts tropicales font partie des écosystèmes les plus riches de la planète, et pourraient concentrer jusqu'à 90 % de l'ensemble des espèces terrestres (Burley, 2002). La diversité taxonomique des arbres peut varier de 22 espèces/ha en Inde à 254 espèces/ha en Equateur, et se traduit par une importante diversité fonctionnelle. Les variations interspécifiques de la composition chimique et de la structure physique des feuilles sont considérables en forêt tropicale humide (Townsend *et al.*, 2008). Par exemple, la variation de la stœchiométrie N:P des feuilles vertes au sein des communautés est extraordinairement importante, et peut excéder la gamme de variation enregistrée sur l'ensemble des arbres du biome tempéré (Townsend *et al.*, 2007). Dans un site forestier de l'île Kauai (Hawaii), Martin et Asner (2009) mettent en évidence que la gamme de variation interspécifique de la signature chimique des feuilles n'atteint jamais de point de saturation avec l'augmentation du nombre d'espèces. Cette diversité chimique est en partie héritée dans les litières et peut même être exacerbée au moment de la sénescence à travers le processus de résorption foliaire. Par exemple, il a été montré en forêt de Guyane française qu'il existait de fortes différences interspécifiques dans la résorption du P parmi des espèces d'arbres co-existentes conduisant ainsi à une variation de la stœchiométrie N:P des litières encore plus importante que celle des feuilles vertes (Hättenschwiler *et al.*, 2008).

Ainsi, la grande diversité spécifique et fonctionnelle des arbres en forêt tropicale humide se traduit localement par une forte hétérogénéité chimique des apports de litières foliaires au sol. Cependant, la compréhension des effets de cette variation interspécifique de la qualité des litières sur la décomposition et le recyclage est encore difficilement appréhendée.

V. Questions et hypothèses

Au cours de cette thèse, je me suis intéressée au rôle de la diversité fonctionnelle des litières issues des arbres dans le processus de décomposition en forêt tropicale humide de Guyane française. Il s'agit de comprendre comment d'une part, la variabilité des traits de la ressource organique, et d'autre part, comment les mélanges de litière de qualité contrastée influencent le processus de décomposition et les organismes décomposeurs. Les grandes questions reliées à ces deux aspects sont présentée ci dessous.

1) Comment la qualité des litières contrôle la décomposition ? (chapitre 1 et 2)

Des études antérieures en forêt de Guyane française (Coq *et al.*, 2010; Hättenschwiler & Jorgensen, 2010) suggéraient que les décomposeurs pourraient être primairement limités en énergie à travers une pauvre qualité de C. En effet, les taux de décomposition n'apparaissaient pas reliés au contenu en nutriments des feuilles, et, notamment non reliés au contenu en phosphore des feuilles, un élément supposé particulièrement limitant à la fois pour les plantes et les organismes décomposeurs en forêt tropicale humide (Cleveland *et al.*, 2002). En revanche, différentes formes biochimiques du C, généralement peu mesurées comme paramètre de qualité des litières, se sont avérées fortement corrélées aux taux de décomposition. Le contenu en formes riches en énergie et facilement accessibles dans les litières (sucres, amidon, phénols de faible poids moléculaire) ont été montrées comme étant positivement corrélées aux taux de décomposition (Hättenschwiler & Bracht Jorgensen, 2010). A l'inverse, la variation interspécifique des tanins condensés dans les litières corrélaient négativement avec les taux de décomposition (Coq *et al.*, 2010). En se basant sur ces études, Hättenschwiler et collaborateurs (2011) (Cf. Annexe A) proposent que la décomposition dans notre système d'étude serait primairement contrôlée à la fois par l'énergie facilement disponible et/ou des mécanismes d'inhibition des organismes décomposeurs (*via* les composés secondaires tels que les tannins).

Pour tester à la fois l'hypothèse d'une limitation primaire en énergie (par la qualité du C) et d'une limitation secondaire en nutriments des organismes décomposeurs, une approche expérimentale basée sur des ajouts factoriels de cellulose, d'azote et de phosphore à des litières de différentes espèces ou des mélanges a été mise en place en laboratoire (chapitre 1) et en forêt naturelle (chapitre 2).

2) Comment la diversité des litières influence la décomposition ? (chapitre 3 et 4)

De nombreuses études mettent en évidence que la diversité des litières influence la décomposition (Gartner & Cardon, 2004 ; Hättenschwiler *et al.*, 2005). Alors que le nombre d'espèces n'a généralement pas d'effet, l'identité et des combinaisons particulières de certaines espèces peuvent largement contrôler ce processus (Wardle *et al.*, 1997). Dans la plupart des mélanges de litières, les taux de décomposition diffèrent de ceux prédits à partir de la décomposition des espèces seules, et la majorité de ces effets sont synergiques (Gartner & Cardon, 2004). Les mécanismes de ces effets-non additifs des mélanges sont encore peu compris.

Nous avons cherché à explorer ces mécanismes en forêt tropicale humide à partir d'approches basées sur les traits des litières. Le 3ème chapitre pose la question du rôle de la dissimilarité stœchiométrique des mélanges de litières sur la décomposition. Notre hypothèse était que la dissimilarité stœchiométrique favoriserait un meilleur équilibre nutritionnel pour les communautés de décomposeurs. Enfin dans le 4ème chapitre, nous avons cherché à expliquer les effets non-additifs des mélanges par la diversité chimique, en prenant également en compte des effets à long terme des espèces d'arbres contribuant aux mélanges.

VI. Contexte de l'étude et cadre expérimental

1- Site d'étude :

Seul territoire français d'outre-mer situé sur le continent sud-américain, la Guyane se situe entre le 2ème et le 6ème degré de latitude nord et entre le 51ème et le 55ème degré de longitude ouest. D'une superficie de 91 000 km², la Guyane est le plus vaste département forestier français. En effet, les formations forestières occupent 96.7% du territoire. La Guyane se trouve dans une zone de circulation atmosphérique Est-Ouest induite par deux ceintures anticycloniques subtropicales (Açores-Atlantique Nord et Sainte Hélène-Atlantique Sud) qui s'affrontent au niveau de la Zone Intertropicale de Convergence (ZIC). Elle bénéficie d'un climat de type équatorial humide. Le cycle saisonnier peut être caractérisée par quatre saisons de durée inégale: (1) Une petite saison des pluies de mi-novembre à fin janvier caractérisé par des pluies modérées (27% du total annuel). (2) Une petite saison sèche également appelé « petit été de mars » (de quelques jours à quelques semaines) se produisant en général entre début février et mi-mars. (3) Une grande saison des pluies de fin mars à fin juillet marquée par de forte précipitations (61% du total annuel). (4) Une grande saison sèche de fin juillet à mi-novembre. Sur l'ensemble de la Guyane, la pluviométrie annuelle est de 3000 mm en moyenne sur la bande côtière, et de 2500 mm dans les régions de l'intérieur.

Le site expérimental de Paracou est localisé en forêt tropicale humide primaire à 20 km au sud de Sinnamary (5°15'N, 53° O). La richesse spécifique est de l'ordre de 140 essences par ha^{-1} pour une densité moyenne de 620 arbres ha^{-1}. La forêt est dominée par les familles des Chrysobalanaceae, Caesalpiniaceae et Sapotaceae. La hauteur moyenne des arbres oscille entre 30 et 40 m et certains arbres émergents peuvent atteindre 50 m (Oldeman, 1974). Le relief de la zone est composé par un ensemble de petites collines pouvant présenter des pentes fortes, et séparées les unes des autres par un réseau hydrographique dense qui draine vers l'Ouest les eaux de pluie dans le bassin versant du Sinnamary. Les sols sont en majorité des oxisols implantés sur une formation métamorphique précambrienne appelée série de Bonidoro. Ce support géologique est constitué de schistes et de grès localement croisés par des veines de pegmatite, d'aplite et de quartz (Epron *et al.*, 2006).

2- La démarche expérimentale :

L'ensemble de la thèse reposant sur des approches expérimentales multifactorielles, différents compromis expérimentaux étaient nécessaires. Dans les trois premiers chapitres, les expérimentations en laboratoire et *in situ* (en forêt) étaient basées sur des ajouts factoriels de carbone, d'azote et de phosphore combinés à différents types de litières décomposant seules (en laboratoire) et/ou en mélanges (*in situ*). En termes d'effort expérimental, ces dispositifs factoriels limitaient la possibilité d'inclure un grand nombre d'espèces. Six espèces (Fig 6) et 14 combinaisons de ces 6 espèces ont donc été sélectionnées. Afin de contrôler les variations liées à la qualité initiale des litières (et plus particulièrement de leur stœchiométrie C: N:P) à partir de ce petit nombre d'espèces, la gamme de variations de la stœchiométrie initiale a été maximisée, de façon à assurer une répartition équilibrée (i) des valeurs moyennes de C : N : P mais aussi (ii) des espèces le long de cette gamme.

Figure 6: Canopées et litières des six espèces d'arbres de forêt tropicale Guyanaise utilisées dans les expérimentations des chapitres 1,2 et 3 de cette thèse.

Chapitre 1

Contraintes stœchiométriques sur les micro-organismes décomposeurs

Figure 7: Microcosmes dans lesquels sont incubées les différentes litières avec les ajouts de ressources C, N, P pendant six mois. Cette expérimentation a été mise en place afin de comprendre les contraintes énergétiques et nutritives exercées par la qualité de différentes litières (aux stœchiométries C : N : P différentes) sur les microorganismes décomposeurs.

Stoichiometric constraints on tropical microbial decomposers

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Introduction

Carbon (C), nitrogen (N) and phosphorus (P) are quantitatively among the 6 major elements in biomass and represent key resources for the metabolic activity of living organisms (Sterner & Elser, 2002). The balance of these elements are known to be particularly constraint in phytoplankton biomass (Redfield, 1958) and the relative constancy of the C:N:P ratio in the world's oceans stimulated the development of a rich stoichiometrically explicit framework of ecological interactions and biogeochemical cycles in marine ecosystems (Elser & Hassett, 1994; Downing, 1997; Sterner & Elser, 2002). Ecological stoichiometry is less studied in terrestrial ecosystems (Elser *et al.*, 2000) and appears to be more complex than in the marine environment, with notably lacking regularities in C:N:P stoichiometry of primary producers (Mcgroddy *et al.*, 2004a). However, there is some evidence for stoichiometric constraints in terrestrial food webs (Elser *et al.*, 2000) with implications for biogeochemical cycles. For example, detrital decomposition, a key process of ecosystem functioning, is known to be under significant stoichiometric control (Swift *et al.*, 1979; Enriquez *et al.*, 1993; Smith, 2002). The carbon to nutrient ratios of primary producers and their litter are considerably higher than those of decomposers (Hessen *et al.*, 2004; Cleveland & Liptzin, 2007) imposing limitations to decomposer growth and activity. Comparing a large number of studies reporting decomposition rates of tissues from different photosynthetic organisms ranging from unicellular algae to trees, Enriquez *et al.* (1993) showed a strong control of plant litter C:N:P stoichiometry on decomposition, with slower decomposition for litter types poor in N or P relative to C. The ratio between the major nutrients N and P also appear as an important determinant of plant litter decomposition, since it influences the relative importance of fungi and bacteria in litter-associated communities and litter nutrient dynamics (Gusewell & Gessner, 2009).

Nitrogen to phosphorus ratios in forest foliage globally increase with decreasing latitude (Reich & Oleksyn, 2004), a pattern that may in part reflect the high age and weathered status of tropical soils consequently impoverished in rock-derived mineral nutrients such as P (Walker & Syers, 1976; Vitousek *et al.*, 2010). However, despite low soil P availability of some tropical soils, recent reports showed considerable heterogeneity in leaf C:N:P ratios among coexisting tree species (Townsend *et al.*, 2007; Hättenschwiler *et al.*,

2008), suggesting a wide range of plant strategies in nutrient acquisition and use in order to cope with nutrient limitation (Hättenschwiler *et al.*, 2011). The high stoichiometric diversity in the tree canopy of tropical forests results in a highly diverse litter input to the soil (Hättenschwiler *et al.*, 2008) creating a mosaic of stoichiometrically diverse resources for soil food webs. Such variability in litter layer quality explains up to a substantial 50% of the variation in potential microbial respiration in the underlying soil in an Amazonian rainforest of French Guiana (Fanin *et al.*, 2011). However, potential microbial respiration was only weakly correlated with litter layer C:N:P stoichiometry. Interestingly, decomposition of a wide range of leaf litter types from this forest correlates well with condensed tannins, phenolics and labile C compounds, but not with the common stoichiometry-related predictors such as C:N and lignin: N (Coq *et al.*, 2010; Hättenschwiler *et al.*, 2011). These findings do not easily fit into the tight relationship between litter C:N:P stoichiometry and decomposition presented by Enriquez *et al.* (1993) and they don't seem to support stoichiometric control of trophic interactions during decomposition as predicted by ecological stoichiometry (Sterner & Elser, 2002). On the other hand, mixtures of different litter types from the same tropical forest of French Guiana varying along a stoichiometric dissimilarity gradient showed a somewhat faster decomposition of stoichiometrically more dissimilar litter mixtures (Hättenschwiler & Bracht Jørgensen 2010). Still, even in these litter mixtures with contrasting stoichiometry, carbon quality apparently was the most important driver of decomposition (Hättenschwiler & Bracht Jørgensen 2010). Collectively, these data suggest that decomposer communities in this tropical rainforest are primarily limited by appropriate C sources to cover their energetic requirements, and that substrate C: N: P stoichiometry plays a minor role. How and to what extent C quality is influencing C: N: P stoichiometry control during decomposition is generally not well studied. However, this may be a key for a better understanding of stoichiometric control on trophic interactions in the terrestrial decomposer food web where heterogeneous and recalcitrant C sources dominate much more than in aquatic food webs.

Here we tested the impact of substrate stoichiometry on microbial decomposer resource use and activity with a laboratory experiment using leaf litter from six tree species of the tropical rainforest of French Guiana separated along a C:N:P stoichiometry gradient. These stoichiometrically distinct natural resources were amended with a relatively easily

accessible source of C in form of cellulose in order to provide microorganisms with a litter independent energy source. We also included a nutrient addition treatment where we added mineral forms of N and P, therefore providing a litter independent nutrient source. Carbon, N and P additions were applied in all possible combinations with the aim to distinguish between absolute and relative stoichiometric constraints as a function of variable stoichiometry of natural resources. We hypothesized that (i) the addition of a relatively easily accessible C source in form of cellulose alleviates energy limitation of microbial decomposers leading to higher microbial activity, biomass and decomposition of tree leaf litter, (ii) external additions of mineral nutrients stimulates the activity and biomass of microorganisms and litter decomposition relatively more on leaf litter with wider C: N: P ratios.

Material and methods

Plant material

We used leaf litter from six tree species occurring in the Amazonian rainforest of French Guiana (*Carapa procera*, *Goupia Glabra*, *Hymenea courbaril*, *Platonia insignis*, *Simarouba amara* and *Vochysia guianensis)*. These six species were selected according to their leaf litter C:N:P stoichiometry in order to represent a gradient of C:N, C:P and N:P ratios (Table 1). Freshly fallen leaf litter of each species was collected in an experimental plantation set up by the French research center CIRAD (Coopération Internationale en Recherche Agronomique pour le Développement), within a natural forest at the Paracou experimental station in French Guiana (5°18′ N, 52°53′ W). In this plantation, a total of 16 tree species formed 25-yr-old mono-specific stands with a fully closed canopy (see Roy *et al.*, 2005 for more details). Freshly fallen litter of each of the six chosen species was collected twice a month during the year 2009 in litter traps suspended in each mono-specific tree stand. Litter traps covered approximately a total area of 25 m^2 allowing a representative sampling at the stand level. Leaf litter was air-dried immediately upon collection in the field, pooled across sampling dates and stored dry. The litter from each individual species was homogenized, and only intact leaves without signs of herbivory, galls or fungal attack or with atypical texture or color were chosen for the experiment.

Experimental design and treatment application

Leaf litter from all six tree species was incubated individually during 240 days in microcosms under controlled conditions in the laboratory. External resource supply of C, N, and P in all possible combinations was used to modify stoichiometric constraints of decomposers. External resources included cellulose (Cellulose powder DS-0, Fluka) for C, NH_4NO_3 and KNO_3 for N, and KH_2PO_4 for P. Cellulose was used as a relatively easily accessible carbon source that can be used by the majority of decomposers (Fontaine *et al.*, 2007), but avoids immediate respiration of for example even more labile sugars. In addition to ammonium nitrate, nitrate was also added as KNO_3 in order to keep the potassium addition constant across the N and P treatment. The seven resource addition treatments (C, N, P, N+P, C+N, C+P, C+N+P) plus a control without supplementary resource addition yielded a total of 240 microcosms (8 treatments x 6 litter species x 5 replicates). Microcosms without litter but with the same resource additions mentioned above were also set up to control for the resource treatment effects on the mixed sand-soil substrate (see below) used to setup the microcosms.

The appropriate quantity of external resources applied to decomposing litter was determined in a preliminary experiment using five different levels of C, N and P based on the average natural annual inputs of C, N and P via leaf litter fall in the studied forest (281g C m^{-2} $year^{-1}$, 6.5g N m^{-2} $year^{-1}$, 0.14g P m^{-2} $year^{-1}$) as the baseline. Leaf litter C, N, P average contents were calculated from data across 45 tree species in the studied forest (Hättenschwiler *et al.,* 2008) and annual leaf litter fall was reported for the year 2004 (Bonal *et al.*, 2008). According to these preliminary tests, optimal C addition was the annual natural C-input to the soil via leaf litter fall (i.e. 281 g C m^{-2} $year^{-1}$ or 1.46 g C per microcosm adjusted for 6 months of experimental duration); optimal N addition corresponded to twice the annual natural N input from leaf litter (i.e. 13 g N m^{-2} $year^{-1}$ or 0.067 g N per microcosm adjusted for 6 months); and optimal P addition corresponded to 50 fold the annual natural P input via leaf litter fall (i.e. 6.9 g P m^{-2} $year^{-1}$ or 0.036 g P per microcosm adjusted for 6 months). The added doses of nutrients were also comparable with nutrient additions used in fertilization experiments in the field of montane tropical rainforests (Hobbie & Vitousek, 2000) and lowland tropical rainforests (Cleveland *et al.*, 2006; Kaspari *et al.*, 2008).

Microcosms consisted of cylindrical plastic boxes of 12 cm height and 11 cm diameter closed with a plastic cap. To each microcosm a mixture of 360 g washed and sterilized sand and 40 g of homogenized topsoil (all plant roots and stones removed by passing through a 2 mm mesh) collected in the natural forest at our study site. The forest soil contained 18.7 g C kg^{-1}, 1.24 g N kg^{-1} and 0.0248 g P kg^{-1} (Hättenschwiler & Bracht Jørgensen 2010). On top of the sand-soil mixture an equivalent of 13 g air-dried leaf litter was added to each microcosm. However, before being added, the litter was first soaked in plastic containers with 250 ml of distilled water for 24 hours in order to completely rewet it. At the end of the soaking period, each container received the treatment specific external resources, was then mixed on a shaker plate during 30 minutes, and was incubated for another 24 hours. At the end of this incubation period, the litter was carefully removed from the container and placed in the respective microcosms on a 1-mm- mesh plastic disk separating leaf litter from the sand-soil substrate. After litter addition, each microcosm was watered with 40 ml of the corresponding incubation solution, ensuring a 80% of the water field capacity, and closed with the plastic cap. Excess water was evaporated at 37°C from the remaining incubation solution and then stored at 4°C until used for the next watering of the corresponding microcosms. The 35 ml incubation solutions were used up after a total of 3 weeks. For all further watering of microcosms during the experiment, deionised water was used. Closed microcosms were kept dark at ambient temperature (29 ± 1.5°C on average) in the laboratory and opened once a week to control for humidity. Humidity was kept constant gravimetrically by watering to reach initial water microcosm weight.

Litter chemistry

For the determination of chemical litter quality (Table 1), subsamples were randomly taken from each species ' initial litter pool, dried at 65°C and ground using a centrifugal mill (Cyclotec Sample Mill; Tecator, Höganäs, Sweden), yielding a powder of uniform particle size of 1 mm. N, P, C, water soluble compounds, cellulose, hemicellulose, lignin, soluble and total phenols, and condensed tannins were measured by Coq *et al.* (2010). We completed these measures with measurements of dissolved organic carbon and non-structural carbohydrates (NSC, i.e. glucose, fructose, saccharose and starch). Sugar and starch were determined following Gomez *et al.* (2007). Briefly, sugar and starch were extracted from 5 mg

of ground litter powder, in the presence of water, methanol and chloroform. After agitation and centrifugation, surnatant (hydroalcoholic phase) was collected to extract sugars (evaporation to dryness for 3h15, solubilization with ultra-pure water) and the remaining solution was used to extract starch (after elimination of surnatant excess, the base was evaporated to dryness for 25 min and solubilized with ultra pure water). The principle of the sugar assay is to follow an enzymatic reaction cascade measured by optical density at 340nm allowing the sequential determination of sugars on a microplate reader. The starch was hydrolyzed to glucose molecules with a hexokinase and final glucose concentration was measured at 340nm. For the determination of dissolved organic carbon, we took 10ml of the initial soaking solution before additions of external resources (see above) from each plastic container, pooled it in five replicates of 80ml each and filtered the solutions using a 0.2 µm filter paper; 10 ml from each replicate were analyzed for DOC content with a total organic carbon analyzer (TOC-6000; Shimadzu, Japan).

Data collection

Microbial respiration (corresponding to the CO_2 efflux of the whole microcosm, including that of sand-soil substrate and that of leaf litter) was assessed for each microcosm after 70, 120 and 210 days of experimental duration using an infrared gas analyser (Licor Li820). Prior to each measurement, microcosms were opened for 5 minutes and then connected to an airtight measurement chamber. The increase of CO_2 concentration within the microcosm-measurement chamber unit was measured every 4 seconds during 200 seconds. The CO_2 efflux (Es), expressed in µmol C $m^{-2}.s^{-1}$, was then calculated based on the chamber volume (V_{ch}) including the volume between the sand-soil substrate and the top of the microcosm), and surface area (S_{ch}) using the following equation:

$$Es = \frac{\Delta[CO_2]}{\Delta t} * \frac{V_{ch}}{S_{ch}} * \frac{1}{V_m} * \frac{273}{273 + T°_{air}}$$

where $\Delta[CO_2] / \Delta t$ is the CO_2 concentration increase during the 100-200 s period Δt (ppm.s^{-1}), V_m is the molar volume of CO_2 (22.4 L.mol-1), and $T°_{air}$ (°C) is the recorded air temperature at the time of measurement.

Table 1: Leaf litter chemistry across the six litter species. All data refer to % dry matter (Mean ±). N = nitrogen, P = phosphorus, C = Carbon, WSC = water soluble compounds, Cell = cellulose, HemiC = hemicellulose, Sphen = soluble phenolics, Tphen = total phenolics, CT = condensed tannins, NSC = non structural carbohydrates, DOC = Dissolved organic carbon. Part of these data were obtained from Coq *et al.* (2010) (see Material & Methods).

	Carapa	*Goupia*	*Hymenea*	*Platonia*	*Simarouba*	*Vochysia*	*F statistic*
CN	51.7±2.2	42.3±4.1	40.9±1.2	34.5±0.6	45±2.9	49.5±2	$F_{5\text{-}24}$ = 6.7 **
CP	2513.4± 147.4	1561.3±168.6	898.2±36.2	2772.9±153.6	1546.7±111.4	1522.4±86.7	$F_{5\text{-}24}$ = 31.2 ***
NP	48.7±2.9	36.9±1.6	21.9±0.4	80.7±5.6	34.4±0.7	31.1±2.9	$F_{5\text{-}24}$ = 49.9 ***
N	0.94±0.04	1.21±0.13	1.22±0.03	1.42±0.03	1.11±0.07	0.87±0.04	$F_{5\text{-}24}$ = 9.3 ***
P	0.019±0.001	0.033±0.004	0.056±0.002	0.018±0.001	0.032±0.003	0.028±0.002	$F_{5\text{-}24}$ = 40.2 ***
C	48.4±0.2	49.7±0.2	49.7±0.1	49±0.3	49.1±0.1	42.9±0.3	$F_{5\text{-}24}$ = 174.3 ***
ws	32.4±0.3	36.6±0.4	31±1	29.3±0.3	45.4±0.4	34.6±1.1	$F_{5\text{-}24}$ = 70.0 ***
hemiC	7.5±0.5	16.2±0.7	10.3±0.1	23.5±0.7	11.7±0.2	20.1±1.1	$F_{5\text{-}24}$ = 88.0 ***
cell	22.7±0.4	18.8±0.3	22.3±0.6	22.5±0.7	20±0.3	19.7±0.4	$F_{5\text{-}24}$ = 13.4 ***
lign	37.5±0.5	28.4±0.8	36.3±0.7	24.7±1.1	22.8±0.8	25.6±0.4	$F_{5\text{-}24}$ = 71.1 ***
Sphen	2.83±0.2	1.06±0.2	1±0.1	0.99±0.03	4.38±0.2	0.62±0.1	$F_{5\text{-}18}$ = 105.7 ***
Tphen	7.99±0.8	2.81±0.3	4.24±0.4	12.5±0.3	11.03±0.8	4.39±0.4	$F_{5\text{-}18}$ = 55.4 ***
CT	2.78±0.3	0.23±0.1	1.38±0.2	0.13±0.01	2.27±0.1	1.41±0.1	$F_{5\text{-}18}$ = 56.2 ***
NSC	0.19±0.03	0.29±0.01	0.47±0.09	1.38±0.2	0.53±0.03	0.43±0.03	$F_{5\text{-}18}$ = 17.0 ***
DOC	0.59±0.04	1.93±0.11	0.57±0.01	1.46±0.1	1.07±0.03	0.75±0.01	$F_{5\text{-}30}$ = 86.5 ***

After 240 days of incubation, the remaining litter from each microcosm was collected and immediately weighed. Each litter sample was then divided in three subsamples to determine remaining litter mass, microbial biomass and enzyme activities. The subsample used to determine remaining litter mass was weighed immediately, gently rinsed to remove adhering cellulose, dried at 60°C during 48h and then reweighed to determine the fresh-to-dry mass ratio. Percentage mass loss was then calculated for each litter sample as the relative difference between initial and final dry mass.

The subsamples used for microbial biomass determination were air-dried prior to measurements. Microbial biomass was determined using the method of Substrate Induced Respiration (SIR) according to the method described by Anderson and Domsch (1978). For each sample, 1.5 g (air dry weight) of litter was placed in a 150-ml plasma flask sealed with a septum to which 6 ml of a water solution containing 20 mg of C-glucose per g of dry litter

was added. Flasks were incubated at 25° for 6 h, a duration that is short enough to prevent *de novo* synthesis of enzymes. Two 200µl air samples from the head space of flasks were analysed after 2 and 6 h of incubation in order to determine CO_2 concentration by means of a gas chromatograph using a catharometer (VARIAN GC 4900; Varian, Walnut Creek, USA). The amount of CO_2 released within 4h allowed to calculate the SIR expressed in ml of C-CO_2 per g of litter (converted in dry weight at 60°C) per hour. Microbial biomass (in mg C g^{-1} litter) was calculated according to Anderson and Domsch (1978) as follows:

$$C_{mic}\ (\text{mg C g}^{-1}\ \text{litter}) = (\text{ml of C-CO}_2\ \text{g}^{-1}\ \text{litter h}^{-1}) * 40.04 + 0.37$$

From the third subsample, enzyme activities were determined following Güsewell and Freeman (2005) with modifications. All activities were measured on enzyme solutions obtained after extraction of 2 g of fresh litter in 8 ml water and focusing 7 activities related to the acquisition of (1) relatively easily accessible C, such as cellulases, hemicellulases, β-glucosidases (2) more complex C compounds, such as laccases, peroxidases, and (3) nutrients such as chitobiases (N acquisition), and phosphatases (P acquisition). For β-glucosidases, chitobiases and phosphatases, 500 µl of extract were incubated 2h at 20°C with 250 µl of methylumbelliferyl (MUF) substrate (400 µM of 4-MUF-β-glucoside for β-glucosidases; 400 µM of 4-MUF-N-acetyl-β-D-glucosaminide for chitobiases and 200 µM of 4-MUF-phosphate for acid and alkaline phosphatases ; Sigma-Aldrich Chemie, Steinheim, Germany). After centrifugation, fluorescence of 200 µl of supernatant was measured at 355 nm (excitation) and 460 nm (emission). Enzyme activities were expressed as µmol of substrate converted.g^{-1} initial dry mass litter.h^{-1}. For cellulases and hemicellulases, 0.2 ml of enzyme extract were incubated with 0.2 ml remazol brilliant blue solution (CM-cellulose 4M in Na-acetate 2M, pH 4.5 for cellulases and 1% w/v azo-xylan in Na-acetate 2M, pH 4.5 for hemicellulases, Megazyme). After 1 h (cellulases) and 4h (hemicellulases) at 40°C, solution was precipitated (5% w/v Na-acetate, 3 H_2O, 0.05 % w/v Zn-acetate 2 H_2O in ethanol 95, pH 5) and centrifuged. Absorbance was determined on 200 µl of supernatants at 590 nm and compared to calibration curves established with a solution of remazol brilliant blue (RBB, Megazyme) in Na-acetate buffer. Enzyme activities were expressed as µmol of RBB. g^{-1} initial dry mass litter.h^{-1}. For laccases, 20 µl of enzyme extract was incubated 4h at 25°C with 160 µl Na-acetate buffer (100 mM, pH 5) and 20 µl of ABTS solution (50 mM in Na-acetate buffer, 2,2-

azino-bis 3-ethylbenzthiazoline-6-sulphonate, Fluka). Absorbance was determined at 420 nm, including boiled samples as control. Laccases activity was expressed in μmol of ABTS production g^{-1}. initial dry mass litter. h^{-1} with an extinction coefficient of 0.36 at 420 nm. Total peroxidases activities were measured as followed: 50 μl of sample were incubated 4h with 10 μl H_2O_2 and 140 μl of substrate solution (MnSO4 1mM, 50 mM 3-dimethylaminobenzoic acid (DMAB), 1 mM 3-methyl-2-benzothiazoline hydrazone hydrochloride (MBTH), Fluka). Absorbance was determined at 420 nm, including boiled samples as control. Enzyme activities were expressed as μmol of DMAB and/or MBTH converted $.g^{-1}$ initial dry mass litter. h^{-1} with an extinction coefficient of 0.32. All measurements were done using a Victor 3 M spectrophotometer (Wallac Perkin-Elmer, Life Sciences, Villebon-Sur-Yvette, France).

Data analysis

Most variables were log-transformed before statistical analysis to obtain normally distributed error terms with homogeneous variance. One microcosm was removed from data due to an outlayer value in mass loss, as the result of a suspicious contamination. The activity values of each enzymes were transformed on a scale of 0-1 by dividing each observation by the maximum activity recorded for that enzyme in the whole set of samples because the order of magnitude of the values for the different enzyme activities varied largely. Enzymes activities were divided into 3 categories according the MARCIE (Microbial Allocation of Resources Among Community Indicators Enzymes) model (Sinsabaugh & Moorhead, 1994): EP (standardized phosphatase activity), EN (standardized chitobiase activity), EC (calculated as the standardized mean activity of the five lignocellulose enzymes assayed). EC were also divided between hydrolytic (ECs) and oxidative (ECc) activities. ECs included glucosidase, cellulase and hemicellulase involved in simple C acquisition and ECc included laccase and peroxidase corresponding to complex C acquisition. In additions, ratios between each group of enzymes were calculated as EN:EP, EC:EP , EC:EN, ECs:ECc.

Two-way ANOVAs was used to test for differences in mass loss, microbial biomass and enzymes activities among species and among resource addition treatments allowing interactions between these two factors. Microbial respiration data were prior analyzed with a linear model using generalized least squares (gls) method which take into account both errors with unequal variances and the non-independence of temporal observations (*i.e*

repeated measures) in estimation of variance-covariance matrix. Species identity, resource supply and time were treated as factors and the variance-covariance matrix structure was specified as autoregressive and heterogeneous. Although the time altered microbial respiration (trough an overall decrease over the course of experiment) and interacted with the other factors (species and resource supply), the effects of resource supply for each species remained generally the same at the three measure times. Consequently, we used a two-way ANOVA on the averages across the three times with species identity and resource supply effect as factors. After all ANOVAs, multiple comparisons to detect overall differences among species and among resource supply were analysed with post -hoc test of Tukey HSD. Because most of the interactions between litter species identity and resource addition treatments were significant, and because species effects were generally higher than resource addition effects, separate ANOVAs for each litter species were run, followed by TukeyHSD to assess specific among resource addition effects. A net resource supply effect on mass loss, microbial respiration and biomass was computed as difference between the mean value in resource amended treatments and the mean value of control treatment mass loss in order to test if the magnitude of the response of mass loss to external resource supply could be related to initial litter quality parameters. Relationships between net resource supply effect and initial litter quality were explored with linear regression analyses. Simple linear models were also used to test correlations between mass loss without resource additions and initial litter quality or correlations between all variables across all data set. The R package (version 2.4.0; R Development Core Package 2006) was used for statistical analyses.

Results

LITTER MASS LOSS

Initial litter quality control on litter mass loss without resource addition

Leaf litter mass loss varied between 18% and 48% of initial litter dry mass among the six tree species when decomposing without resource addition (Fig. 1a). *Goupia* leaf litter decomposed the fastest and mass loss decreased in the order of *Goupia* > *Platonia* > *Simarouba* > *Hymenea* > *Vochysia* > *Carapa*. Of all the measured initial litter quality traits, initial concentrations in DOC and in condensed tannins correlated best with litter mass loss. Initial DOC was positively (r^2 = 0.84**, Fig.1b) and condensed tannins negatively (r^2 =0.65, *P* = 0.054, Fig. 1c) correlated with mass loss, respectively. There was no significant correlation between mass loss and initial litter C:N, C:P or N:P ratios.

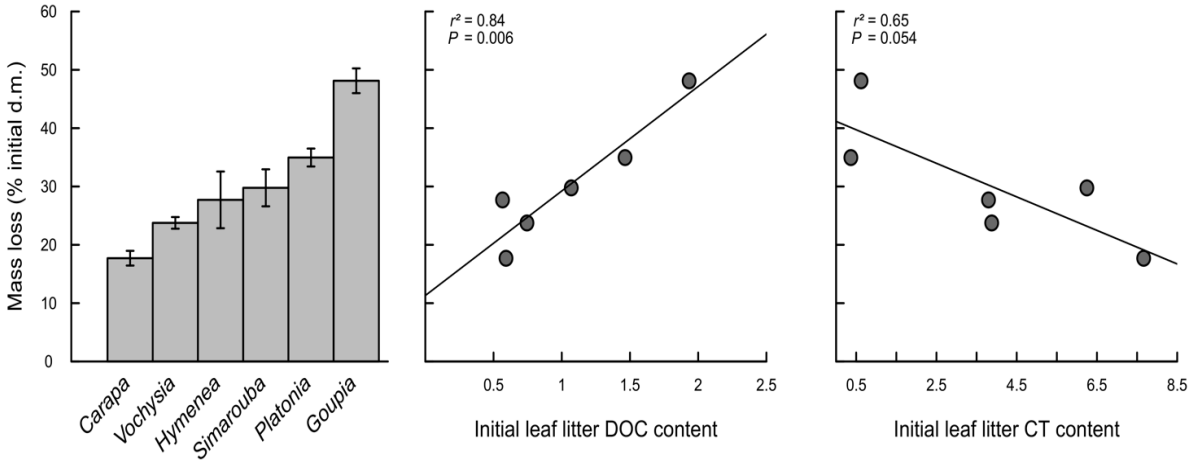

Figure 1: Litter mass loss (expressed in % of initial dry matter) without external resource addition as function of a) species identity b) initial concentration in dissolved organic carbon (expressed in % of initial dry matter), and c) initial concentration in condensed tannins (expressed in % of initial dry matter).

Table 2: Results of ANOVA to test for the effects of litter species (S) and resource supply (R) treatments on mass loss, microbial respiration and microbial biomass. % SS represent the percent of sum squares, Sum Sq = sum squares, %SS = % sum squares (representing the variance partition), Mean Sq = mean square, *** = p-value <0.001.

	Factors	Df	Sum Sq	%SS	Mean Sq	F value
Mass loss	Species (S)	5	17.4	54.3	3.5	118.2 ***
	Resource (R)	7	6.2	19.5	0.9	30.3 ***
	S * R	35	2.8	8.6	1.0	2. 7 ***
	Residuals	191	5.7	17.6	0.03	
Microbial respiration	Species (S)	5	18.0	21.7	3.6	51.6 ***
	Resource (R)	7	44.2	53.4	6.3	90.4 ***
	S * R	35	7.2	8.7	0.2	3.0 ***
	Residuals	191	13.4	16.2	0.07	
Microbial biomass	Species (S)	5	41.9	55.1	8.4	201.7 ***
	Ressource (R)	7	17.0	22.27	2.4	58.2 ***
	S * R	35	9.3	12.18	0.3	6.4 ***
	Residuals	191	7.9	10.4	0.04	

Effects of resource supply on leaf litter mass loss

Apart of species identity, litter mass loss was affected by external resource supply, which however depended on litter species (Table 2). Overall, the combined addition of external N and P stimulated litter mass loss, whereas additions of N or P alone had no effect on litter mass loss. However, the NP effect varied among litter species (Fig. 2) with significant increases in litter mass loss in the three species *Carapa*, *Platonia* and *Vochysia*, with up to 59% higher mass loss (*Platonia)* with combined additions of N and P compared to the control. *Goupia* leaf litter mass loss tended to increase with combined N and P addition, but not significantly (P = 0.87). *Hymenea* and *Simarouba* leaf litter did not even show a trend of response to any external nutrient additions. A net NP supply effect was calculated as the difference between the mean mass loss in the +NP treatment and in the control treatment. Most of the initial litter quality traits were not correlated to this NP supply effect (data not shown). However, total initial litter P concentration (r^2 = 0.89**), N:P (r^2 = 0.83* , Fig. 3) and C:P ratios (r^2 = 0.89**) correlated positively with the NP supply effect on mass loss. *Platonia* (one of the tannin-poor and DOC-rich rapidly decomposing species) as well as *Carapa* (a tannin-rich and DOC-poor slowly decomposing species) were the two species that showed the strongest NP supply effect (Fig. 3).

In contrast to nutrient supply, external C additions in the form of cellulose did rather slow litter mass loss with the exception of a stimulating trend on *Goupia* litter mass loss when N and P were added simultaneously (Fig. 2).

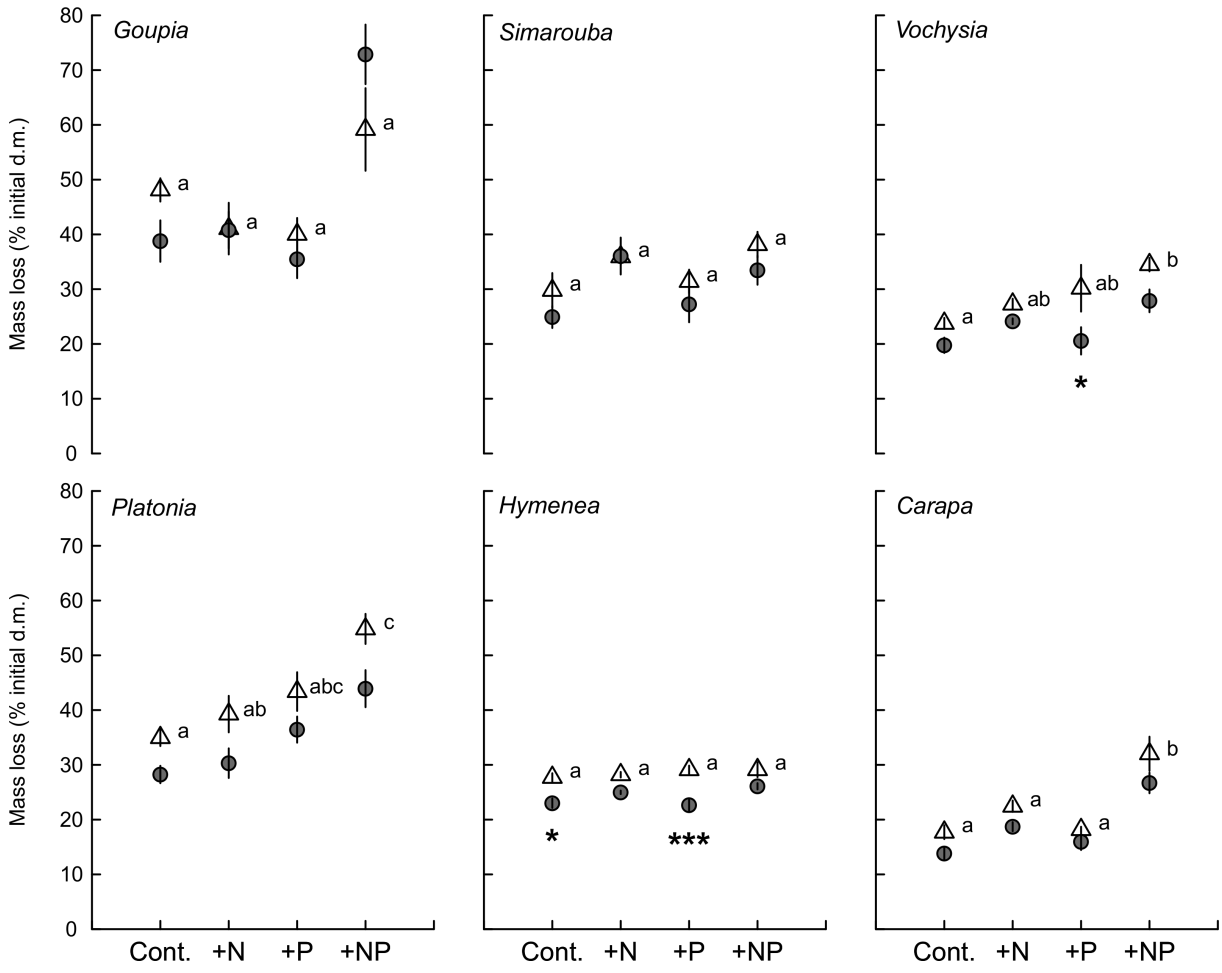

Figure 2: Effect of external resource supply on litter mass loss (expressed in % of initial dry matter) for each species. Cont. = control treatment (without resource addition). Triangles represent treatments without C and circles correspond to C treatments. Symbols denote the level of significance of Tukey HSD multiple comparisons; different letters indicate mass loss values that differed between nutrient-amended treatments and control, stars denote the level of significance between CN *vs* N, CP *vs* P, and CNP *vs* NP mass loss values (. <0.1, * <0.05, **<0.01, *<0.001).**

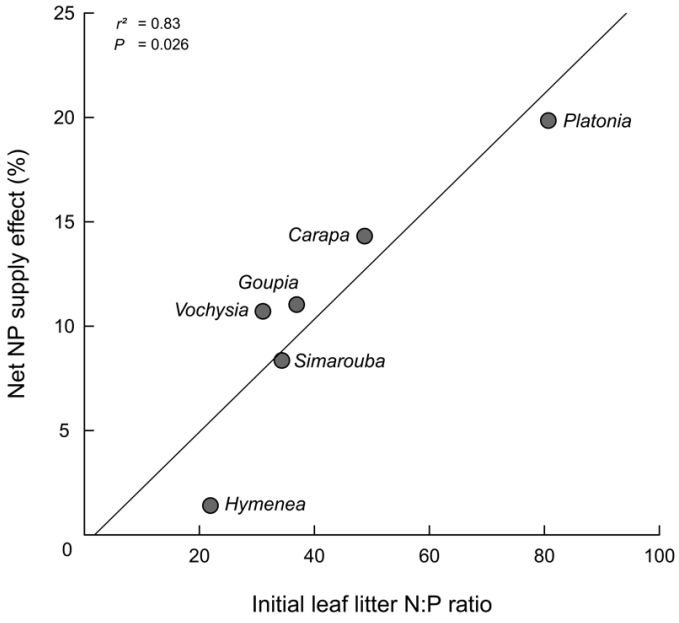

Figure 3: Observed effect of NP treatment (computed as the mean value between mass loss for NP treatment minus mass loss for control) as a function of the initial leaf litter N:P stoichiometry.

MICROBIAL FUNCTIONING

Litter species effects

Microbial respiration and biomass, and enzyme activities were all affected by litter species identity (Table 2, Table 3). The species effect on microbial respiration, biomass and ECs:ECc ratio was generally the same, with the two most rapidly decomposing species *Platonia* and *Goupia* showing the highest microbial respiration (respectively 2.3 and 2.1 µmol C m^{-2}. s^{-1} on average across all treatments) and biomass (respectively 5.9 and 7.4 mg microbial C g^{-1} litter on average) and the lowest ECs:ECc ratio (respectively 2.2 and 1.4 on average). In contrast, the slowly decomposing species *Vochysia* and *Carapa* displayed the lowest microbial respiration (respectively 1 and 1.2 µmol C $m^{-2}.s^{-1}$ on average) and biomass (2.2 and 4.1 mg C g^{-1} litter on average) and the highest ECs:ECc ratios (2.9 and 4.9 on average). Microbial respiration and biomass were positively correlated with litter mass loss ($r^2 = 0.16^{***}$ and $r^2 = 0.36^{***}$, respectively), and ECs:ECc ratio was negatively correlated with litter mass loss ($r^2 = 0.31^{***}$), reflecting the distinct species responses. Allocation towards N-, and P- acquisition enzymes varied also among litter species (Table 3) but did not show any

clear pattern relative to litter species-specific litter mass loss, microbial respiration or biomass (data not shown).

Effects of nutrient supply

Microbial respiration and biomass, and enzyme activities were all affected by resource addition and their interactions with litter species identity (Table 2, Table 3). The combined N and P addition (but not of that of N or P alone) stimulated microbial respiration compared to control treatments for *Platonia* (+151% on average), *Goupia* (+122% on average), *Carapa* (+99% on average) and *Vochysia* leaf litter (+43%), but not for *Hymenea* and *Simarouba* leaf litter (Fig. 4). The overall effects of additions of P alone and in combination with N (but not of N alone) resulted in higher microbial biomass compared to control treatments (Fig. 5). The effect of P addition alone on microbial biomass was significant for *Platonia* and *Vochysia* leaf litter only, while the combined addition of N and P stimulated microbial biomass in *Platonia*, *Vochysia*, and *Carapa* leaf litter and as a non-significant trend in *Goupia* leaf litter (Fig. 5). The effect of a combined NP addition on microbial respiration and microbial biomass depended on the initial litter N:P ratio in the same way as was observed for litter mass loss. The effect of NP addition on microbial respiration and biomass was stronger with higher initial litter N:P ratios (r^2= 0.83* and r^2 = 0.74*, respectively).

The addition of external nutrients also significantly affected ECs, ECc, EN and EP enzyme activities as well as their ratios (Table 3). P additions consistently reduced EP in P and NP treatments compared to controls, whereas EN activity was reduced only in NP treatment (Table 3). The strong reduction of EP resulted in overall higher EN:EP and EC:EP ratios in P and NP treatment compared to controls whereas EC:EN did not vary significantly despite the EN reduction (Table 3). Finally, the ECs:ECc ratio did not significantly vary with nutrient treatments but tended to decrease when P was added (both P and NP) due to a significant decrease of ECs compared to the control treatment (Table 3). Even though the effects of nutrient additions interacted to some extent with species identity, the effects showed largely the same patterns across species, with the interaction due to non-significant effects for some species (data not shown).

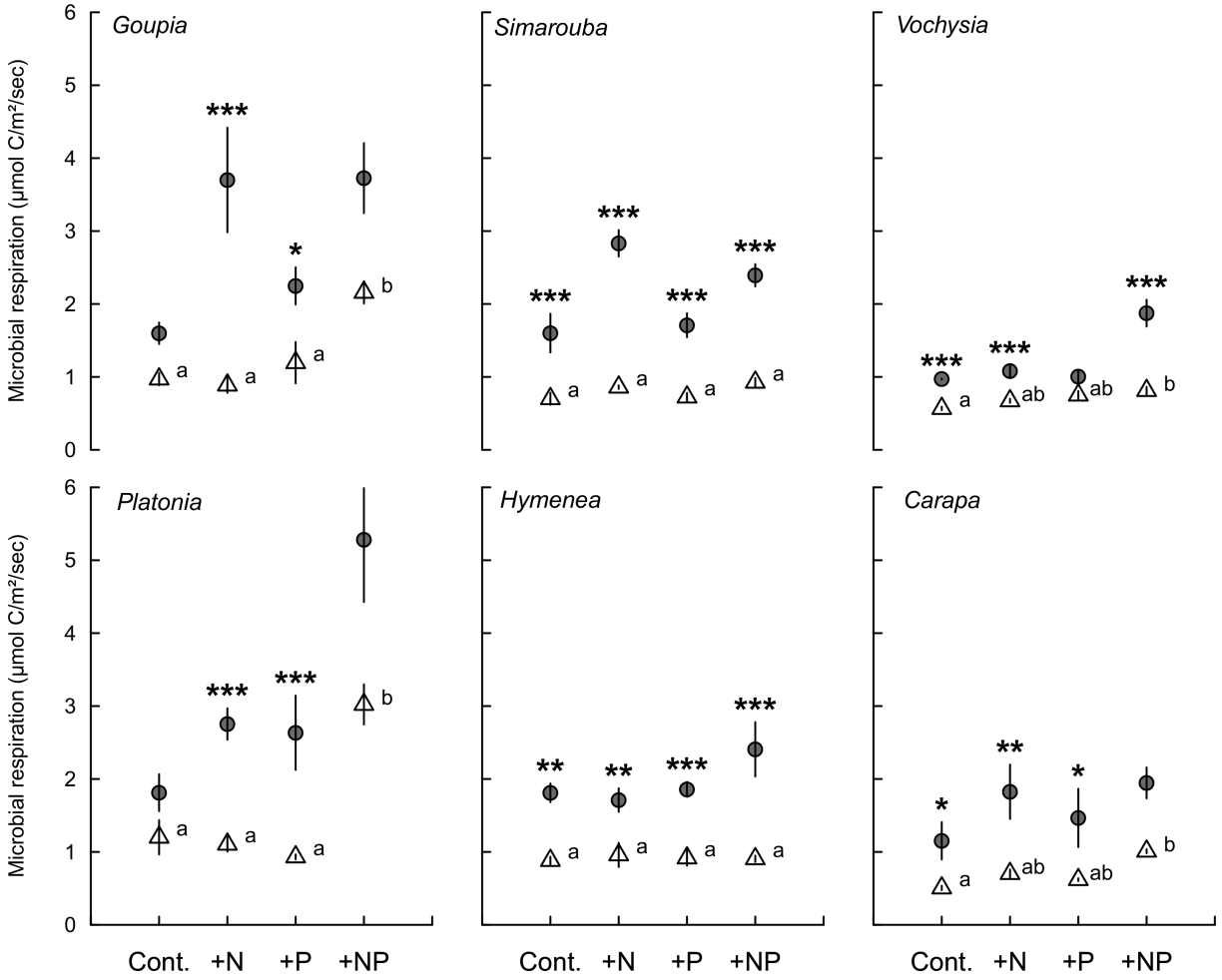

Figure 4: Effect of resource supply on microbial respiration (expressed in µmol C.m^{-2}.sec^{-1}) Cont. = control treatment (without resource addition). Triangles represent treatments without C and circles correspond to C treatments. Symbols denote the level of significance of TukeyHSD multiple comparisons; letters denote the level of significance of TukeyHSD multiple comparisons to test if microbial respiration in nutrient treatments differed from control treatment and stars denote the level of significance of multiple TukeyHSD comparisons CN *vs* N, CP *vs* P, CNP *vs* NP (. <0.1, * <0.05, **<0.01, *<0.001).**

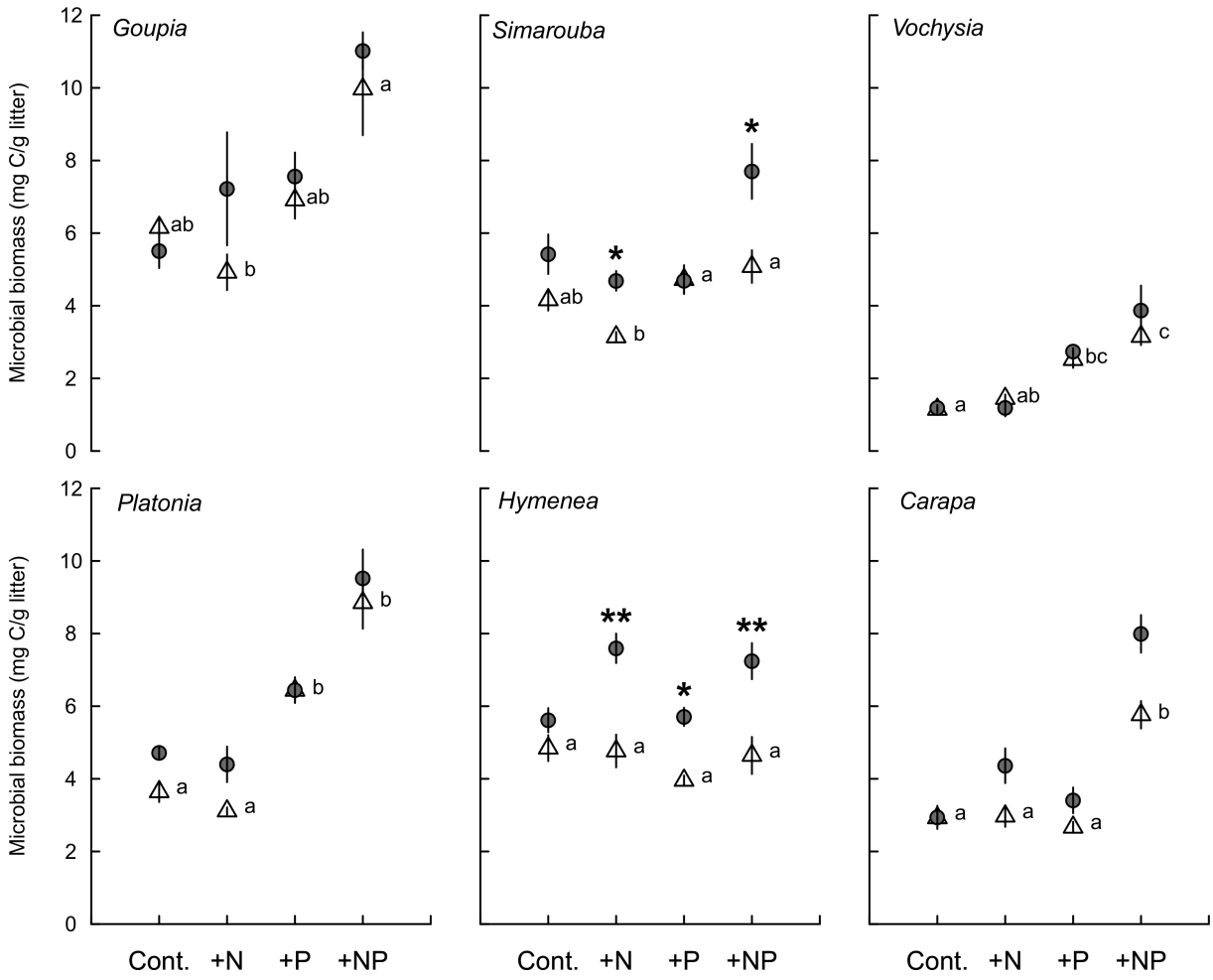

Figure 5: Effect of resource supply on microbial biomass (expressed in mg C g^{-1} litter) Cont. = control treatment (without resource addition). Triangles represent treatments without C and circles correspond to C treatments. Symbols denote the level of significance of TukeyHSD multiple comparisons; letters denote the level of significance of TukeyHSD multiple comparisons to test if microbial biomass in nutrient treatments differed from control treatment and stars denote the level of significance of multiple TukeyHSD comparisons CN *vs* N, CP *vs* P, CNP *vs* NP (. <0.1, * <0.05, **<0.01, *<0.001).**

Table 3: Results of ANOVA to test for the effects of litter species(S) and resource supply treatment (T) on enzyme activities and their ratios. Different letters denote significant difference between species or between nutrient-treated compared to control. Stars denote for significant differences between C *vs* T, CN *vs* N, CP *vs* T, CNP *vs* NP.

		EN	EP	EN:EP	EC:EN	EC:EP	Ecs	ECc	Ecs:ECc
Factors	df	*F*	*F*	*F*	*F*	*F*	*F*	*F*	*F*
Species (S)	5	17.9***	89.0***	34.0***	17.9***	96.5***	40.1***	49.2***	74.4***
Resource (R)	7	12.2***	121.1***	43.5***	7.3***	101.1***	21.0***	11.6***	11.4***
S * R	35	2.3**	4.9***	4.9***	2.2**	6.2***	3.1***	1.4	2.0*
Overall effect of Resource supply									
Cont.		0.14 ^{ab}	0.35 ^{a}	0.51 ^{a}	4.21 ^{a}	1.68 ^{a}	0.41 ^{a}	0.18 ^{a}	3.13 ^{a}
N		0.2 ^{a}	0.42 ^{a}	0.45 ^{a}	3.21 ^{a}	1.16 ^{a}	0.44 ^{a}	0.15 ^{a}	3.51 ^{a}
P		0.1 ^{bc}	0.13 ^{b}	1.43 ^{b}	4.04 ^{a}	5.2 ^{b}	0.37 ^{b}	0.16 ^{a}	3.0 ^{a}
NP		0.08 ^{c}	0.1 ^{c}	1.5 ^{b}	5.97 ^{a}	6.7 ^{b}	0.34 ^{b}	0.16 ^{a}	2.87 ^{a}
C		0.18	0.46 *	0.44	2.72	1.03	0.42	0.26 *	2.49 *
CN		0.31	0.41	0.73 *	3.02	1.53	0.42	0.23 *	2.17 *
CP		0.12	0.13	1.27	3.58	4.09	0.37	0.18	2.7
CNP		0.15 *	0.14	1.98	3.64 *	6.74	0.36	0.21 *	2.13 *

Effects of carbon supply on microbial functioning

C addition strongly stimulated microbial respiration in most cases (Fig. 4). Addition of C alone stimulated microbial respiration in *Carapa* (+128%), *Simarouba* (+128%), *Hymenea* (+105%), and *Vochysia* (+71%) leaf litter, but not in *Platonia* and *Goupia* compared to the control treatment (Fig. 4). All litter species showed a strong increase in microbial respiration with the combined additions of C and nutrients compared to nutrient treatments (Fig 4.). In contrast, C additions had only very limited effects on microbial biomass (Fig. 5). With the addition of C alone, microbial biomass did not change significantly, and multiple comparisons between CN *vs* N, CP *vs* P, and CNP *vs* NP treatments showed very little effects of C addition on microbial biomass with the exception of *Hymenea* and *Simarouba* leaf litter (Fig. 5).

The overall effect of the addition of C alone resulted in higher EP compared to the control, but EP did not change with the combined addition of carbon and nutrients

compared to respective nutrient only treatments (Table 3). The overall effects of C, CN and CNP treatments resulted in higher ECc activities compared to control, N and NP treatments, respectively, leading to an overall lower ECs:ECc ratio (Table 3). Despite the significant interaction between resource supply and species identity (Table 3), the same trends were generally observed across species (data not shown).

Discussion

The high variation in leaf litter stoichiometry observed in the tree species-rich tropical forest of French Guiana is thought to have important consequences for resource use of microbial decomposer communities (Hättenschwiler *et al.*, 2008). At the same time there is clear evidence that these communities are limited by accessible C sources (Hättenschwiler *et al.*, 2011) which suggests a complex interdependence of C quality and stoichiometry control on decomposers. The idea of C quality/energy limitation at our study site is in line with the positive correlation between litter DOC that can be easily assimilated by microorganisms (Moorhead & Sinsabaugh, 2006), and decomposition across the six stoichiometrically distinct litter types used in our study. Accordingly, we hypothesized that if a relatively easily accessible energy source in form of cellulose is added to the natural litter, its decomposition will be accelerated because at least part of the microbial decomposers can use cellulose or intermediate products during cellulose degradation to cover their energetic needs. Cellulose is the main constituent of leaf litter tissues, but is mostly bound up in lignin, pectin and waxes and, consequently, litter cellulose breakdown first needs a degradation of recalcitrant C-compounds which was not required here with pure cellulose addition (Baldrian, 2008). The comparatively easily accessible cellulose could then act as a priming compound (Kuzyakov *et al.*, 2000; Fontaine *et al.*, 2007), which would then allow the breakdown of the more complex C compounds of the litter material and microbial access to litter nutrients. The data from our 240-day microcosm experiment did not confirm this hypothesis. Instead of accelerating litter decomposition, cellulose addition rather slowed decomposition of natural litter and did not change microbial biomass regardless of species identity of the litter material. The lack of cellulose effect was not due to a microbial community that was incapable to use cellulose as growth substrate since we measured highly stimulated

microbial respiration with cellulose additions in four out of the six litter species. While cellulose apparently was respired by microorganisms it did not stimulate the breakdown of the more complex natural litter material as the priming effect would predict. Fontaine *et al.* (2007) proposed that a priming effect occurs when microorganisms with a K-strategy (high C-use efficiency) become more competitive than those with a r-strategy (low C-use efficiency). Apparently, in our study cellulose addition may have primarily stimulated microorganisms with low C-use efficiencies (*i.e.* a low C fixation in biomass compared to respired C) that are inefficient in the breakdown of recalcitrant C. In the longer term however, competitive interactions in the microbial community could eventually result in a priming effect as indicated by cellulose-induced shifts in enzyme activities leading to lower ECs : ECc ratios. This shift suggests less expression of enzymes targeting relatively simple C compounds at the expense of more expression of enzymes capable to break down more complex C compounds.

According to stoichiometric theory we stated in our second hypothesis that the addition of mineral forms of the two key nutrients N and P would increasingly stimulate microbial activity and decomposition of litter with widening C: N: P ratios. Litter inherent C:N:P stoichiometry did not correlate with either litter mass loss or microbial biomass/activity without external resource addition. However, the combined addition of mineral N and P clearly stimulated litter mass loss and microbial biomass/activity as a function of initial leaf litter N: P stoichiometry. The wider initial litter N: P stoichiometry was, the stronger the combined addition of mineral N and P stimulated litter mass loss. In other words, decomposition of leaf litter with a relatively narrow N: P ratio closer to that of microbial biomass is less accelerated by supposedly unlimited mineral N and P. In line with our hypothesis this is clear evidence for litter stoichiometry control over decomposer activity.

The N:P ratio is widely considered as a good indicator of plant nutrient status and the kind of nutrient limitation for plant growth (Koerselman & Meuleman, 1996; Agren, 2008) as well as for decomposition (Smith, 2002; Gusewell & Freeman, 2005). Leaf N: P ratios above a threshold of about 15 to 22 (on a mass basis) should indicate P limitation to biomass production and decomposition, while ratios that are below of about 14 should rather indicate N limitation (Smith, 2002; Tessier & Raynal, 2003; Gusewell, 2004). Since the range in N: P

ratios covered by our six litter species was between 21.9 and 80.7 we would expect P rather than N limitation. However, with the exception of the particularly P-poor *Platonia* litter, P addition alone did not stimulate decomposition in any of the litter species regardless of their initial N: P ratio. Only a high external availability of both P and N led to the observed increased decomposition as a function of initial litter N: P. In fact, mineral N availability may initially be more important than mineral P availability even though P is more limiting in absolute terms. This is because microbial mineralization and acquisition of N from leaf litter material requires the breakdown of the C skeleton of organic compounds while that of P does not (Schimel & Bennett, 2004; Craine *et al.*, 2007). Therefore P is lost from decomposing litter material at higher rates than N (Hättenschwiler & Bracht Jørgensen 2010) and is at least initially relatively more accessible. As a consequence, N addition is a prerequisite for mineral P supply to have an effect. The responses to nutrient additions observed for microbial biomass and activity were largely in line with those for litter mass loss. These results confirm that the observed increase of litter mass loss as a function of litter N:P ratio were driven by a more abundant and active microbial community when external mineral N and P were available. The trend of a positive effect on *Platonia* leaf litter mass loss with P addition only was even stronger and statistically significant for microbial biomass.

The activity of N and P acquiring enzymes decreased in the NP treatment in accordance with several studies showing an inhibition of chitobiase or phosphatase with N and/or P supply, respectively (Kang & Freeman, 1999; Olander & Vitousek, 2000; Sinsabaugh *et al.*, 2002). However, we did not observe a shift towards higher activities of C-acquiring enzymes in the NP treatment. In contrary, simple C acquiring enzymes generally decreased with combined additions of N and P whereas complex Carbon acquiring enzyme activities remained relatively constant. Probably, a more fine temporal resolution of enzyme activities should provide a better insight on the relation between external nutrient supply and C enzyme allocation.

Chapitre 2

Les effets des fertilisations C, N, P sur la décomposition en forêt Amazonienne

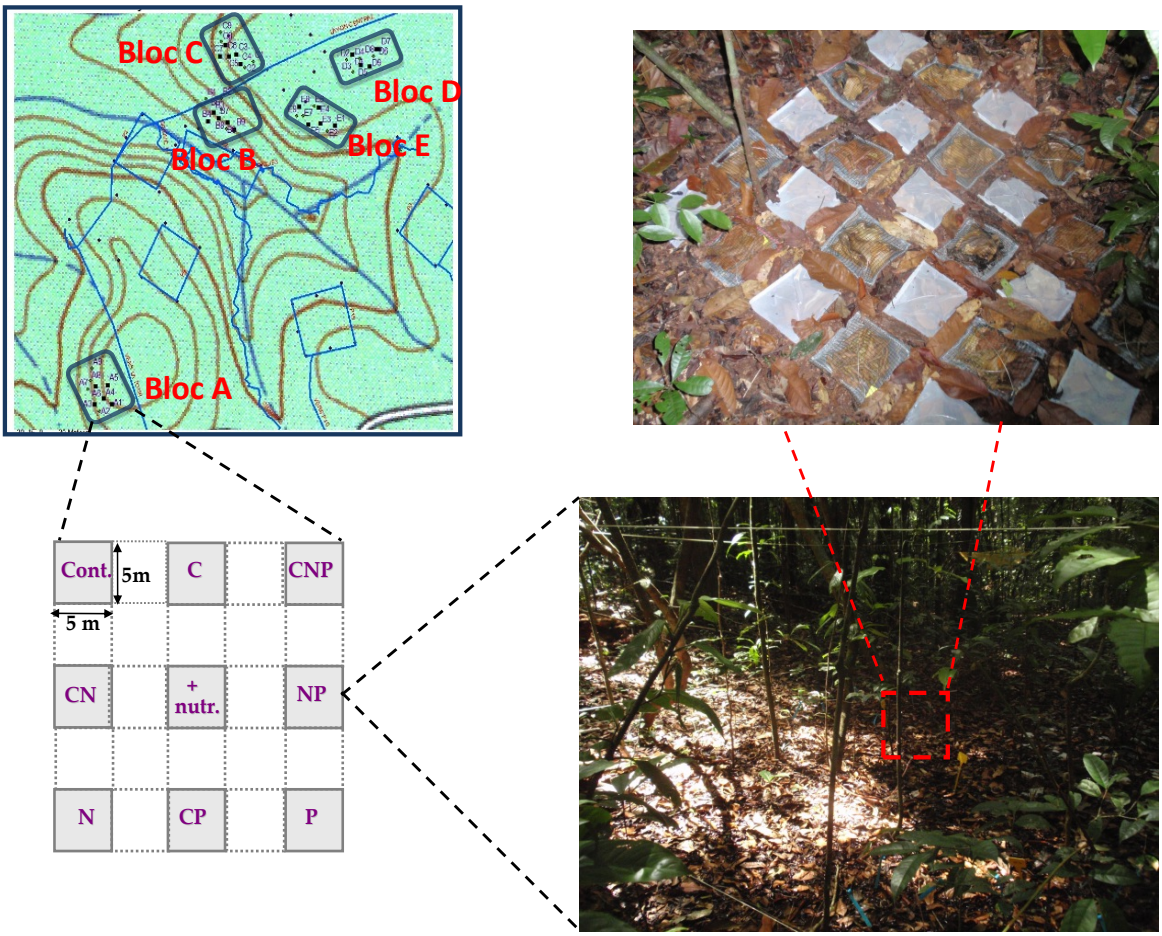

Figure 8: Dispositif expérimental de fertilisation en C, N, P installé *in situ* en forêt naturelle de Paracou en Guyane française. Toutes les combinaisons possibles d'ajouts de C,N,P ainsi qu'un traitement supplémentaire de cations majeurs et micronutriments (nutr.) et un traitement contrôle (sans aucun ajout) ont été effectués au sein d'un plan en bloc complet (5 blocs). Des sachets de litières contenant des espèces seules de litières ou différentes combinaisons parmi 6 espèces de litières ont été installés au sein de chacune des placettes. Les sachets, suivant la taille de leur maille, permettaient ou non l'accès de la méso- et de la macrofaune aux litières. Au total 1800 sachets de litières ont été installés.

C, N, P-fertilization effects on decomposition in an Amazonian rainforest

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Introduction

Tropical forests play a key role in regulating Earth's climate and biogeochemical cycles, notably the carbon cycle (Luyssaert *et al.,* 2007; Malhi *et al.,* 2008). Although their global importance is well recognized, the limiting factors for primary productivity and elemental cycling are still poorly understood for the structurally and geologically highly diverse tropical forests and much less studied than in temperate forests (Townsend *et al.,* 2008). Soils at low latitudes are often very old and highly weathered, with little initial bedrock derived nutrients left (Vitousek *et al.,* 2010; Walker & Syers, 1976). Phosphorus (P) availability decreases over time due to leaching, occlusion with secondary minerals and the formation of recalcitrant soil organic matter (Vitousek *et al.,* 2010). In contrast, significant stocks of N accumulate over the long term through biological N_2 fixation (Hedin *et al.,* 2009), resulting in the widespread belief that P rather than N limit ecosystem processes in tropical rainforests. Some indirect evidence along natural soil P gradients and direct evidence with experimental nutrient additions showed that P predominantly limit ecosystem processes on old tropical soils, such as in Borneo (Paoli *et al.,* 2005), Hawaii, (Herbert & Fownes, 1995; Hobbie & Vitousek, 2000), or Costa Rica (Cleveland *et al.,* 2002; Cleveland *et al.,* 2006). However, Cuevas and Medina (1988) emphasized earlier that the type of nutrient limitation can change dramatically within Amazonian rainforests of Venezuela depending on soil type, with Tierra Firme forests particularly Ca- and Mg- limited, whereas other forest types (Tall Caatinga and low Bana forests) were mainly N-limited. Recently, Kaspari *et al.* (2008) highlighted that potassium and other micronutrients rather than P limit litter fall and decomposition in a Panamanian rainforest. The strong abiotic heterogeneity among tropical rainforests (with particularly wide range of soil age and weathering status) but also the high biotic diversity, and thus the important potential for plant species-driven variation in nutrient cycling (Townsend *et al.,* 2008) is a big challenge for the generalisation of a simple P limitation for the functioning of tropical rainforests. Experimental evidence of nutrient limitation remains particularly scarce in theses ecosystems, especially with respect to litter decomposition as a key process of ecosystem functioning.

Climate conditions are highly favourable for decomposers in warm and humid tropical ecosystems. Decomposer activity is therefore under relatively stronger control of plant-derived organic matter as their main source of energy and nutrients (Lavelle *et al.,*

1993). Although leaf litter material is rich in total C roughly accounting for 40% of total leaf litter dry matter, a large part of this C is available in complex and recalcitrant compounds difficult to access by decomposers. An extensive body of literature highlights that recalcitrant C forms such as lignin impose a predominant control over decomposition, slowing down leaf litter breakdown across different biomes (Swift *et al.* 1979; Melillo *et al.,* 1982; Berg & Laskowski, 2006). Beyond this well documented C quality or energetic constraint of lignin, the role of C availability on leaf litter decomposition has been largely neglected, despite the fact that C substrate identity (such as sugars, polysaccharides, or phenolics) strongly alters soil microbial driven processes (Orwin *et al.*, 2006). The stimulation of microbial breakdown of relatively old and recalcitrant soil organic matter by the addition of energy-rich and easily accessible C compounds known as the priming effect (Fontaine *et al.,* 2007; Kuzyakov *et al.,* 2007; Blagodatsky *et al.,* 2010), additionally highlights the potential of important interactions among different C compounds and their net effect on the soil C balance. Moreover, recent studies in the tropical rainforest of French Guiana showed that quantitatively minor groups of C compounds such as non-structural carbohydrates, soluble phenols and condensed tannins drive interspecific variation in leaf litter mass loss (Hättenschwiler & Bracht Jørgensen, 2010). In a recent review, Hättenschwiler *et al.* (2011) argued that a syndrome of poor litter C quality evolved in nutrient poor Amazonian rainforests imposing energy starvation on decomposers to increase plant access to limiting nutrients.

Apparently, the availability of both nutrients and relatively labile C compounds can play a major role for decomposition in tropical rainforests, but their relative importance is not understood. With a combined experimental fertilization with N in the form of urea, mineral P and a relatively easily accessible C source in the form of cellulose we tested the relative importance of these resources on the decomposition of a range of different litter substrates in an undisturbed rainforest of French Guiana. We added these external resources singly and in all possible combinations to test for co-limitations and interactions among resources in a randomized complete block design. Leaf litter from six different native tree species and different mixtures thereof was used in order to represent the wide range of litter chemistry among tree species in this forest at small local scales (Hättenschwiler *et al.*, 2008). Based on previous studies in the same forest (Hättenschwiler *et al.,* 2011), we hypothesized

that i) the decomposer community is primarily energy limited and that the external addition of cellulose as a relatively easily available C substrate should alleviate energy limitation and thus increases litter decomposition, that (ii) additional nutrient fertilization (in particular P) further stimulates decomposition, because it should compensate for imbalanced stoichiometry of litter substrates.

Materials and methods

Site description and fertilization design

The study site is located in an Amazonian undisturbed rainforest at the Paracou experimental station in French Guiana (5°18′ N, 52°53′ W). The climate is tropical wet, mainly driven by the north/ south movement of the Inter-Tropical Convergence Zone (ITCZ), characterized by a long-term average annual temperature of 26 °C (1971-2001) and an average annual precipitation of 3,041 mm (1971-2001). Temperature varies only little over the course of the year, but variations in precipitation are substantial with less rainfall during two rather dry periods in March and from mid-August to mid-November (Gourlet-Fleury *et al.,* 2004). The forest is characterized by a tree species richness of about 140 species ha^{-1} with a mean density of 620 individual trees ha^{-1} (individuals of a diameter > 0.1 m at breast height) and an average tree height of 35m (Bonal *et al.,* 2008). Soils are nutrient-poor acrisol developed on a Precambrian metamorphic formation called the Bonidoro series and composed of schist sand-stone. The mean pH is 4.7 in this study site. Soil samples have been harvested before fertilization for further standard soil physical and chemical analyses (Fanin *et al.,* 2011) and despite some variations, soil parameters are roughly comparable across the five blocks. Soil texture was clay-sandy with 74% of sand on average (varied from 67% to 79% across the five blocks) and 19.7% of clay on average ranged from 15.6 to 24.1%. The soil C content was 22.1 mg C. g^{-1} dry soil on average across the five blocks (ranged from 18.7 to 26.7), the soil N content was 1.5 mg N. g^{-1} dry soil (ranged from 1.3 to 1.8) and the soil P total content varied from 0.08 mg P. g^{-1} dry soil to 0.13 mg P. g^{-1} dry (0.10 on average). The soil Fe and Al were respectively 20.4 mg Fe. g^{-1} soil and 42.7 mg Al. g^{-1} soil (Fanin *et al.*, 2011).

To test the effects of resource availability on decomposition, a fully factorial fertilization experiment was set up with C, N, P supply in all possible combinations. Because

the nutrient limitation of decomposers could be more complex than just N or P limitation (Kaspari *et al.,* 2008; Townsend *et al.,* 2008), we also added an additional fertilization treatment including the major cations (K, Ca, Mg) and micronutrients (i.e. B, Cu, Fe, Mn, Mo, S, Zn). These eight treatments plus a control (without fertilization) were applied to 5.5 x 5.5 m plots within five blocks (a total of 45 plots, each receiving one of the nine treatments and repeated across the 5 blocks). Plots within blocks were separated by at least 5 m distance and distances among neighbour blocks ranged between 50 m and 300 m. The five blocks were established on even terrain to avoid lateral losses of added resources by runoff, within a rather homogeneous zone. The appropriate quantity of external resources (*i.e* non-limiting for decomposition) to be applied to litter was determined in a preliminary experiment using five different levels of C, N and P based on the average natural annual inputs of C, N and P via leaf litter fall in the studied forest (281g C m^{-2} $year^{-1}$, 6.5g N m^{-2} $year^{-1}$, 0.14g P m^{-2} $year^{-1}$) as the baseline. Leaf litter C, N, P average contents were calculated from data across 45 tree species in the studied forest (Hättenschwiler *et al.,* 2008) and annual leaf litter fall was reported for the year 2004 (Bonal *et al.,* 2008). According to these preliminary tests, optimal C addition was 0.5 times the annual natural C-input to the soil via leaf litter fall (i.e. 1405 kg C ha^{-1} $year^{-1}$ added as cellulose (commercial susbtrate Waterspare, celliob industry, FRANCE). N addition corresponded to twice the annual natural N input from leaf litter (i.e. 130 kg N ha^{-1} $year^{-1}$ as coated urea [$(NH_2)_2CO$]), and P addition to 50 fold the annual natural P input via leaf litter fall (i.e. 69 kg P ha^{-1} $year^{-1}$ as [KH_2PO_4]). Plots with micronutrient additions received a liquid micronutrient fertilizer equivalent to 22 kg ha^{-1} $year^{-1}$ consisting of H_3BO_3 (1150 ppm), $CuSO_4$ (1150 ppm), Fe-EDTA (2%), $MnSO_4$ (1150 ppm), $ZnSO_4$ (600 ppm) and $(NH_4)_2MoO_4$ (600 ppm), plus K_2SO_4 equivalent to 87 kg K ha^{-1} $year^{-1}$ and also Ca-EDTA corresponding at 50 kg Ca. ha^{-1} $year^{-1}$. The added doses of nutrients were largely comparable to nutrient additions used in fertilization experiments in the field of montane tropical rainforests (Hobbie & Vitousek, 2000) and lowland tropical rainforests (Cleveland *et al.,* 2006; Kaspari *et al.*, 2008). Fertilizers were applied twice a year during the drier periods (in October and in March-April) and the first fertilization event was initiated in April 2009.

Plant material

Leaf litter from 6 tree species typical for the forests in our study area (*Carapa procera, Goupia glabra, Hymenaea courbaril, Platonia insignis, Simarouba amara,* and *Vochysia tomentosa*) were chosen to represent the high diversity in litter quality among tree species at our study site (Hättenschwiler *et al.,* 2008), and more specifically to illustrate a wide gradient in C:N, C:P, and N:P stoichiometries. Freshly fallen leaf litter of each species was collected in an experimental plantation, adjacent to the natural rainforest, set up in 1983 by the French research centre CIRAD (Coopération Internationale en Recherche Agronomique pour le Développement). In the mono-specific stands of the plantation (see Roy *et al.,* 2005 for more details), leaf litter of each of the six species was collected twice a month during the year 2009 in suspended litter traps. Litter traps covered approximately a total 25 m^2 area for each tree species sampled, allowing a representative sampling at the stand level. Leaf litter was air dried immediately upon collection in the field, pooled across sampling dates and stored dry. The litter from each individual species was homogenized, and only intact leaves without signs of herbivory, galls or fungal attack or with atypical texture or color were chosen for the experiment. Litter quality from these six species has been extensively described in Coq *et al.* (2010) and Barantal *et al.* (in prep), with particularly large differences in the concentration of condensed tannins (from 0.1 to 3.5 % of dry mass), hemicelluloses (from 6.8 % to 27.8 % of dry mass) and phosphorus (from 0.016 to 0.056 % of dry mass).

Litter decomposition

Leaf litter was exposed in the field using litterbags of two different mesh sizes (68 µm and 8 mm mesh bags (DIATEX, St-Genis-Laval, France). Different mesh sizes were used to separate the fauna effect on decomposition, known to be important in our study system (Coq *et al.,* 2010) and to test for potential interactions between fauna effect and resource additions. To avoid losses of litter fragments through the largest mesh width during field exposure, the side of the litterbag facing the surface soil consisted in a 0.5 mm mesh (DIATEX, St-Genis-Laval, France). The 0.15 x 0.15 m large litterbags were filled with 8 g of air-dried leaf litter. Apart of using litter of the six individual tree species, we also used litter mixtures consisting of 2, 3, 4, or 6 species, that better represent the heterogeneous litter layer in the studied

forest. Litter mixtures contained equal amounts of component species and were defined in order to maximize the stoichiometric dissimilarity among all possible mixtures (Barantal *et al.*, in prep), but allowing each of the six species to occur exactly twice in 2, 3 and 4 species mixtures, then ensuring a fully equilibrated representation of all species. These prerequisites for litter mixture constitution yielded a total of 14 litter mixtures (six 2 species-mixtures, four 3-species-mixtures, three 4-species-mixtures, and one mixture including all 6 species).

The totally 40 different litterbag types (20 litter substrates x 2 mesh sizes) were placed randomly from 3 to 11 September 2009, one month before the second fertilization event (the first fertilizer application was in April 2009), in each of the 45 experimental plots (see above) yielding a total of 1800 litterbags. An additional set of litterbags filled with either *Vochysia* or *Goupia* litter was used to assess the effect of mesh size on litter humidity within litterbags. These additional litterbags were exposed in plots with the combined addition of C and P in four out of the five blocks and harvested either during the dry period on 19 November 2009, or during the wet period on 18 January 2010. Litter humidity did not vary between coarse and fine mesh litterbags in the dry season (respectively 44.4% and 42.4% of humidity on average), but was slightly higher in fine mesh (64.6% of humidity on average) than in coarse mesh (57.7% of humidity on average) litterbags during the rainy season.

All litterbags were retrieved after a total of 156 days of field exposure from 9 February to 17 February 2010 in the same order as they have been placed in the field. Upon harvest, remaining litter was gently rinsed with tap water to remove roots, invertebrates and soil particles, dried at 65°C to constant weight and weighed to determine remaining litter mass.

Data analysis

Litter mass loss is expressed in percentage of initial litter oven-dry weight (sub-samples of initial air dried pool litter from each species were taken before placed in bags to determine the air- to oven-dry mass ratio). To investigate the effects of litter substrate identity (20 different litter treatments), resource supply and fauna presence/absence on mass loss, we used a three- way analysis of variance with block effect as additional factor. The ''net nutrient effect'' on mass loss was calculated within each block as the difference in mass loss (i) between nutrient- fertilized plots and control plots (for the effect of nutrient addition

alone), and (ii) between nutrient fertilized plots that additionally received external C and plots that were only fertilized with C (to look at the nutrient effect when C constraint was alleviated). This net nutrient effect was tested using ANOVA with litter substrate identity, C presence/absence, nutrient treatments (+N, +P and +NP), mesh size, and block as factors. The interactions that were not significant ($P > 0.05$) were removed from the model and the analysis was run again. Tukey post hoc tests were used following these two models to explore multiple comparisons of main and interaction terms more specifically. To determine whether the chemical composition of the litter substrates influenced the response of mass loss to the different factors, simple linear regressions were used. Initial litter quality of litter mixtures was calculated as the average from the relative contribution of each species present. The R package (version 2.4.0; R Development Core Package 2006) was used for statistical analyses.

Results

After 160 days of exposure in the field, mass loss ranged between 19.0 and 90.8 % of initial mass with an average of 44.1%. Mass loss was affected by litter treatment (corresponding to the 20 different litter substrates), resource supply, and fauna presence/absence (Table 1). Moreover, the presence/absence of fauna interactively affected mass loss with litter substrate identity and resource supply (Table 1). In addition, a significant block effect was found, that was mainly due to an overall lower mass loss in one out of the five blocks.

Fauna effect

Based on the F-statistics of our general statistical model, the fauna effect was by far the most important explaining most of the variation in litter mass loss (Table 1). In the non-fertilized control plots, the presence of fauna contributed to an average 46.1% increase in mass loss across the different litter treatments (44% increase on average across all data set). However, the fauna effect depended to some extent on litter substrate identity (Table 1). Also, the variation in mass loss among the different litter substrates was higher in the

presence of fauna (CV = 31% among substrates in control plots) than when fauna was excluded (CV= 17%).

Table 1: Anova to test for litter identity, fauna presence/absence and resource supply effects on litter mass loss (% initial dry matter).

	Df	Sum Squares	Mean Squares	F value	Pr(>F)
Litter substrate identity (L)	19	94112.9	4953.3	59.6	< 0.0001
Fauna presence/absence (F)	1	111826.1	111826.1	1345.3	< 0.0001
Resource supply (R)	8	49583.4	6197.9	74.6	< 0.0001
Block	4	4910.2	1227.5	14.8	< 0.0001
L * F	19	46076.1	2425.1	29.2	< 0.0001
L * R	152	14577.3	95.9	1.2	0.1
F * R	8	12115.9	1514.5	18.2	< 0.0001
L * F * R	152	11419.7	75.1	0.9	0.8
Residuals	1420	118038.9	83.13		

Fertilization effect

Fertilization with C, N and P significantly altered mass loss explaining the second most variability in our model (Table 1). It is noteworthy that these fertilization effects were independent of litter substrate identity (no significant interaction, Table 1), i.e. the different litter substrates used in our experiment were similarly affected by fertilization (Table 1). However, the fertilization effect was influenced by the presence of fauna in that fauna generally amplified the fertilization effect. Finally, the three-way interaction between fertilization, litter substrate and fauna was not significant, revealing that the fauna-induced increase in the fertilization effect was similar across the different litter substrates.

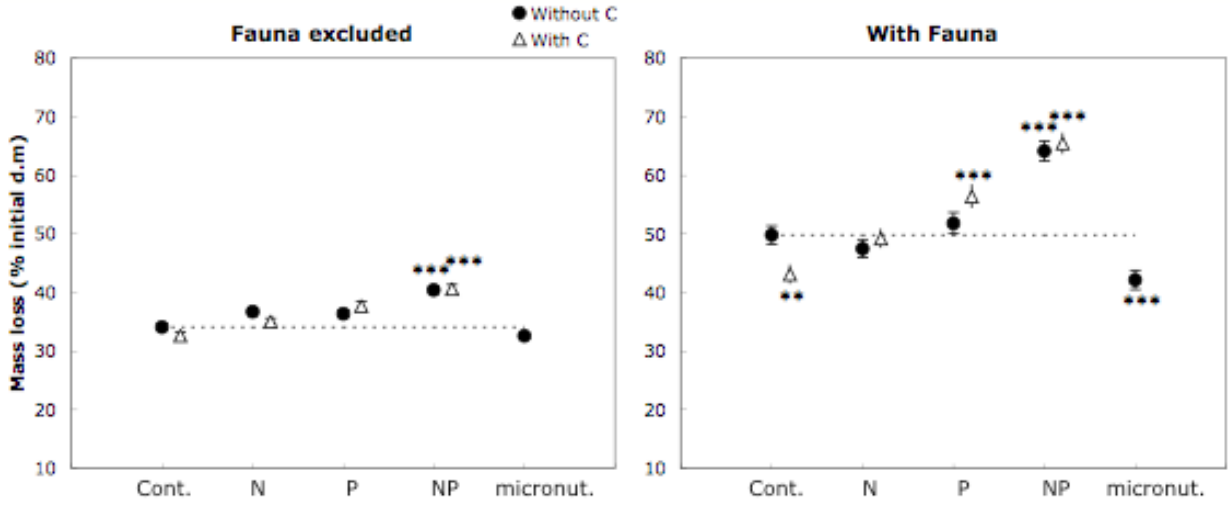

Figure 1: Mass loss (in % of initial dry weight) across the different types of resource added in a) fine mesh and b) coarse mesh litterbags. Stars denote for the level of significance compared to control treatment (. **<0.01, *<0.001), without resource additions (noted Cont.). Blank circles represent treatment without C additions whereas blanck triangles represent the respective nutrient + C additions. The dashed line represents the mean mass loss in control plots.**

Mass loss in N-fertilized plots (36.7% and 47.5% mass loss on average in fine and coarse mesh litterbags, respectively) or in P-fertilized plots (36.3% and 51.8% mass loss on average in fine and coarse mesh litterbags, respectively) did not differ from mass loss in control plots (34% and 49.8% mass loss on average in fine and coarse mesh, respectively, Fig. 1). However, the combined fertilization with both N and P led to an increased mass loss in fine and coarse mesh litterbags compared to control treatment (Fig. 1.). This NP fertilization effect resulted in an average increase of mass loss of 18% and 28% without or with fauna, respectively. The fertilization with micronutrients rather slowed litter decomposition with an average of 4.4% ($P = 0.99$) and 15.3% ($P < 0.0001$) less mass loss compared to control plots in fine and coarse mesh litterbags, respectively (Fig. 1.).

The addition of pure cellulose alone had a rather negative effect on the overall mass loss compared to the control. However, this C effect differed between fine and coarse mesh litterbags with a more negative and significant effect in the presence of fauna (Fig 1). The combined fertilization with C and nutrients generally had no further effects on litter mass loss beyond the effect of nutrient fertilization, with the exception of the marginally significant effect of the combined fertilization with C and P in the presence of fauna (Fig. 1, $P = 0.06$, as compared to P only). Compared to the fertilization with P only, C addition increased mass loss in the presence of fauna by 8.9 %.

The net nutrient effect (see M&M for calculations) showed that an additional C fertilization did not significantly change the effect of nutrient fertilization on mass loss without fauna access (Table 2, Fig 2). However, there was a small trend for increased mass loss with a combined C and P or NP fertilization (Fig. 2). In contrast, when fauna was present, net nutrient effects were consistently and significantly higher with additional C fertilization (Fig 2).

Table 2: Anova to test for the effects of C fertilization (with or without added C), nutrient fertilization (N, P or NP), fauna presence and litter substrate identity on the net nutrient effect.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
C supply (C)	1	9051	9051	54.54	<0.0001
Fauna presence/absence (F)	1	7687.41	7687.41	46.33	<0.0001
Nutrient supply (Nut)	2	24085.44	12042.72	72.57	<0.0001
Litter substrate identity (L)	19	7345.53	386.61	2.33	0.001
block	4	4439.18	1109.8	6.69	<0.0001
C * F	1	4959.89	4959.89	29.89	<0.0001
F * Nut	2	7395.8	3697.9	22.28	<0.0001
C * L	19	5192.5	273.29	1.65	0.04
F * L	19	4955.52	260.82	1.57	0.06
C * F * L	19	6744.86	354.99	2.14	0.003
Residuals	1108	183863.24	165.94		

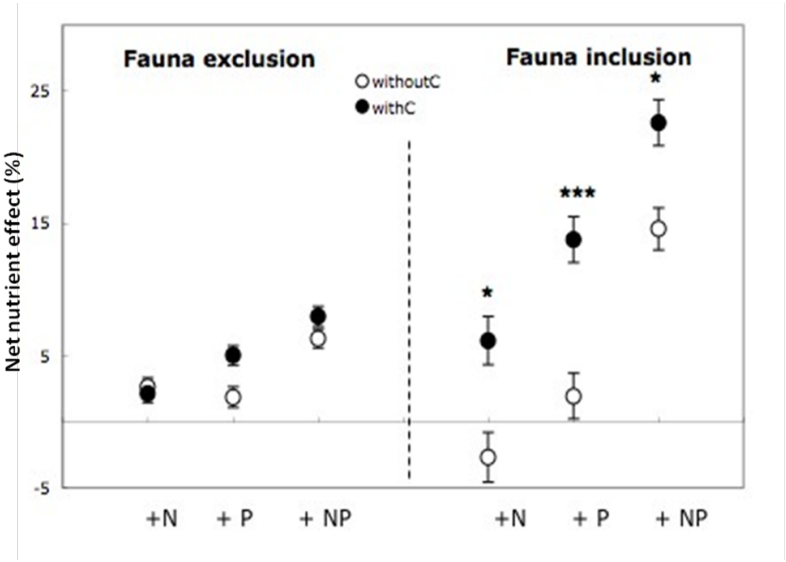

Figure 2: Net nutrient effect in fine and coarse mesh following C supply. Net nutrient effect was calculated as the difference between mass loss in nutrient without or with C supply treatment minus respectively the mass loss in control or C alone treatment. Blank circles represent treatment without C additions whereas black circles represent the respective nutrient + C additions.

Initial litter quality control

The observed effect of litter substrate identity on mass loss is largely driven by distinct litter chemistry among litter types. In order to evaluate how and which litter quality traits were related to mass loss, we explored correlations between chemical composition (mean of chemical traits calculated from component species) and mass loss of non-fertilized litter substrates for fine and coarse mesh litterbags separately. Total litter C concentration correlated best and positively with mass loss when fauna was excluded (r^2=0.52***) and initial litter DOC correlated best and positively (r^2=0.64***) and condensed tannins negatively (r^2= 0.58***) with litter mass loss in the presence of fauna.

The fertilization effects on mass loss were quite robust across the different litter types with no significant interaction between fertilization and litter substrate identity (Table 1). However, depending on the type of fertilization, the mass loss responses to fertilization varied substantially across the different litter substrates. For instance, the effect of NP fertilization varied between 2.6% and 33.5% net increase in mass loss compared to the control treatment in presence of fauna and between 3.5 and 14.8% net increase when fauna was excluded. To further explore these litter type-dependent fertilization effects, linear regressions of the net fertilization effect and initial litter chemistry were evaluated. The slightly negative effects of C or micronutrient fertilization on mass loss were not related to

any initial litter chemistry parameters. The net effects of combined P and C fertilization and of NP fertilization (without and with supplementary C fertilization) were significantly related to the P status of the initial litter substrate (litter P concentration, N:P and C:P ratios).

These relationships were particularly strong for coarse mesh litterbags (Table 3). Moreover, when fauna had access, the response of mass loss to any combination of P fertilization with either N or C or both increased clearly with increasing litter N:P and C:P ratios and with decreasing initial P concentration (Table 3, Fig 3). The same pattern was found when fauna was excluded, however the correlations were weaker (Table 3, Fig 3).

Table 3: Results of linear regressions between the net nutrient effect (see M&M for calculations) on mass loss and initial litter chemistry for both fauna treatments separately. r^2 represent the adjusted r-squared obtained by linear model. P-values for statistically significant relationships are in bold.

	NP effect								P effect (with C)	
	Without C				With C					
	Fine mesh		Coarse Mesh		Fine mesh		Coarse Mesh		Coarse Mesh	
	p-value	r^2	*p-value*	r^2	*p-value*	r^2	*p-value*	r^2	*p-value*	r^2
P	0.3	0.02	**0.029**	0.19	**0.005**	0.33	**<0.0001**	0.56	**0.001**	0.43
CP	0.6	-0.04	**0.025**	0.21	**0.04**	0.17	**0.0021**	0.38	**0.0069**	0.3
NP	0.4	-0.01	**0.0066**	0.31	**0.018**	0.23	**0.018**	0.23	**0.006**	0.31
hemicell	**0.014**	0.25	**0.011**	0.27	**0.002**	0.38	**0.066**	0.13	**0.0037**	0.35
lign	**0.045**	0.16	0.15	0.06	**0.012**	0.26	0.49	0.01	0.11	0.09
CT	0.18	0.05	0.14	0.07	**0.036**	0.18	0.28	0.01	0.1	0.1
NSC	0.17	0.05	**0.013**	0.26	0.09	0.11	0.69	0.01	0.09	0.11
DOC	0.47	-0.02	0.4	-0.01	**0.016**	0.24	0.12	0.08	0.15	0.06

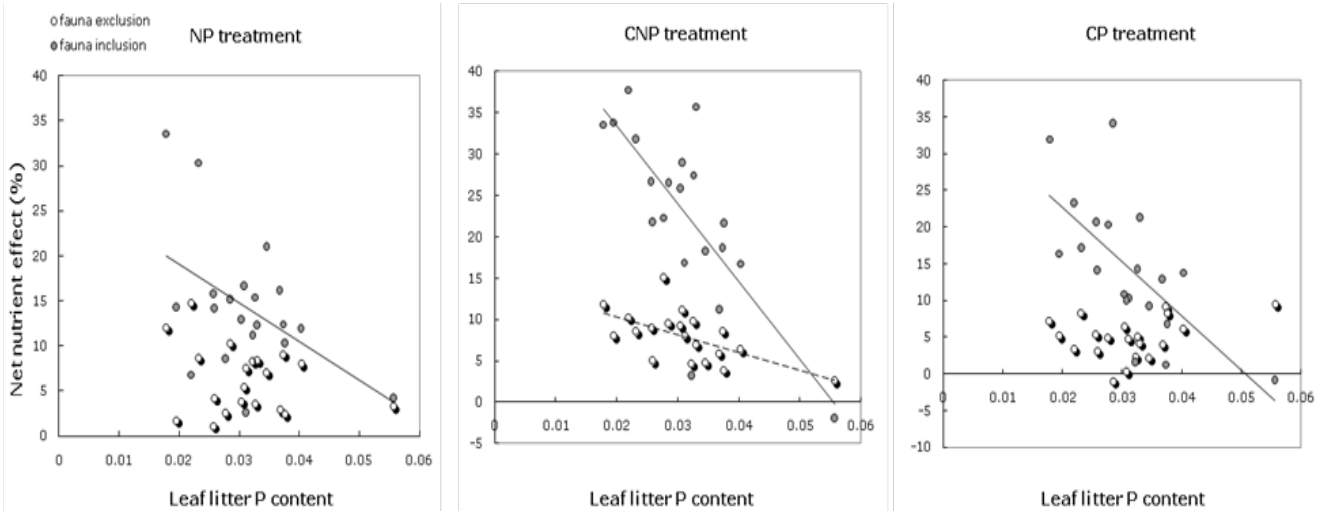

Figure 3: Linear relation between net nutrient effect and P-related traits in fauna presence (grey circles) and without fauna (blank circles).

Discussion

Our field experiment in the tropical rainforest of French Guiana showed that mass loss of litter from different tree species and various mixtures therefore varied strongly in response to fauna presence, litter species composition and fertilization.

The presence of fauna increased the average litter mass loss by 32% in the non–fertilized control plots. While the use of litterbags with different mesh sizes is a common approach for the assessment of the contribution of soil fauna to litter decomposition, it has the inconvenience that part of the fragmented litter material may have been lost through the wider mesh without actually being consumed and metabolized by soil fauna. However, we intended to minimize such loss by the use of a two-sided litterbag with a smaller mesh of 0.5 mm on the soil facing side. Also, according to Anderson (1973) and Bradford *et al.* (2002) such fragmentation and transfer of litter particles to deeper soil layers is part of the soil fauna driven litter mass loss. Our finding of significant fauna contribution to litter decomposition is in line with previous studies that showed a more important fauna contribution to decomposition in tropical ecosystems than in ecosystems at higher latitudes (Gonzalez & Seastedt, 2001; Hättenschwiler *et al.*, 2011; Lavelle *et al.*, 1993; Wall *et al.*, 2008). This latitudinal gradient in fauna contribution was mostly interpreted as an effect of more favourable and stable climatic conditions in tropical ecosystems allowing a more continuous soil fauna activity year round (Heneghan *et al.*, 1998). Like in a previous study at our site (Coq *et al.*, 2010), we found that the fauna effect on decomposition depended on litter substrate identity, indicating that soil fauna shows clear preferences for some litter types.

These preferences appear to be related to C-quality since litter types rich in DOC were more affected and those rich in condensed tannins were less affected by fauna presence which has also been reported by Coq *et al.* (2010) for single species litter from 16 different tree species.

In order to directly test the role of C quality for decomposer communities hypothesized to be the main limiting factor for decomposer activity (Hättenschwiler & Bracht Jørgensen, 2010; Hättenschwiler *et al.,* 2011), we included a "C fertilization" with cellulose addition in our experiment. We expected that cellulose could alleviate energetic constraints on decomposer activity and would stimulate litter mass loss through a priming effect. Our results do not confirm this hypothesis since litter mass loss rather decreased in cellulose-amended plots compared to control plots. This response to cellulose addition suggests that decomposers shifted to a preferential use of the more accessible cellulose compared to the complex litter material with no feedback on litter decomposition at least within the time span of our experiment. Previous studies have shown that increased soil inputs of labile C compounds (sugar, cellulose, or root exudates) do have such feedback effects leading to increasing mineralization rates of recalcitrant organic matter (De Nobili *et al.,* 2001; Fontaine *et al.,* 2007) through the priming effect. However, most of these studies assessed the effect of labile C on soil organic matter (Kuzyakov *et al.,* 2000), and only rarely in decomposing leaf litter (Boberg *et al.,* 2008; Chigineva *et al.,* 2009). Similar to our findings, Chigineva *et al.* (2009) reported a negative effect of sugar addition on leaf litter decomposition in a Russian spruce forest. Sugar addition and slower litter decomposition were associated with an increase in the abundance of opportunistic fungi with an r-strategy while fungi specialized on more recalcitrant substrates typical for a K-strategy decreased in abundance (Chigineva *et al.,* 2009). Such a shift in decomposer community composition obviously prohibited the expression of a priming effect. This may also have been the case in our study, although we intentionally did not use sugar or other highly labile C-compounds to avoid such immediate effects via fast-growing opportunistic microorganisms. In order to better evaluate whether or not a priming effect on litter decomposition could be important in our study system a more detailed analyses of microbial community composition and how it evolves over time would be required. Perhaps in later stages of litter decomposition, microbial community dynamics are different and the consequences of labile C addition would differ.

In combination with nutrient fertilization, however, cellulose addition had a positive effect on litter decomposition. Interestingly, the observed positive net nutrient effect on decomposition was enhanced with a simultaneous C fertilization, in particular when fauna was present. This positive effect of cellulose addition on the net nutrient effect was particularly pronounced in the P treatment, but was also present in the N only and the combined N + P treatments (Fig. 2). These results suggest that a combined increased availability of an easily accessible C source and nutrients provides the required additional resources for the decomposer community for an accelerated breakdown of leaf litter. Apparently the fauna component of the decomposer food web was more responsive to a C + nutrient fertilization than microorganisms. Preliminary results from a detailed soil fauna assessment at our study site in February 2011 indicate that the abundance of earthworms and macroarthropod detritivores increased in the C + P treatments regardless of whether or not N was added as well, compared to the control and compared to the single C or P treatments (J. Nahmani, pers. comm.). Such higher fauna abundance may have contributed to stimulated litter decomposition, but it is difficult to pinpoint the potential mechanisms for this effect. In an earlier study from a temperate beech forest, Scheu and Schaefer (1998) showed that the number and biomass of earthworms increased strongly in response to glucose addition, but not in response to nutrient addition. This result suggests C limitation of earthworms, probably via a strongly stimulated microbial biomass rather than nutrient limitation.

The fact that the combined fertilization with N and P increased litter mass loss by up to 28% without C being added at the same time indicates that decomposers in our study system are not solely limited by C. Apparently N and P are required both for a nutrient effect on decomposition contrary to the expected particularly strong P effect in this highly P impoverished ecosystem. This result is in line with a previous laboratory experiment under controlled conditions without fauna using mono-specific litter from the same six species we exposed here in the field (Barantal *et al.*, unpublished manuscript). It seems that the relatively difficult access to organic N for which the C-skeleton of N containing compounds has to be broken up is limiting any positive P effect. Apparently, only a high external availability of both P and N led to a stimulated decomposition. Our findings do not concur with a previous fertilization experiment in a Panamanian tropical rainforest, where Kaspari

et al. (2008) showed a positive effect of P fertilization on decomposition independently of N fertilization. Moreover, in their study, N fertilization even reduced the stimulatory P effect (Kaspari *et al.,* 2008). Likewise, Cleveland *et al.,* (2006) found in a Costa Rican rainforest a strong P fertilization effect on microbial mineralization of dissolved organic matter, while a N fertilization had a negative effect.

The positive N + P fertilization effect on decomposition depended strongly on litter quality. Litter P status was a particularly strong determinant for the extent of N+P fertilization effects. The N+P fertilization effect on litter mass loss increased with decreasing litter P concentration and with increasing N:P and C:P ratios. The litter species used in our experiment represented a wide range of leaf litter C:N:P stoichiometry (C:P ratio ranged from 900 to 2770 and N:P ratio from 20 to 80). Such strong control of initial litter quality on the fertilization effect on decomposition may in part explain the different results we obtained compared to previous fertilization experiments in tropical forests. For instance, the leaf litter used by Cleveland *et al.* (2006) had significantly lower C:P (344 to 512) and N:P (14 to 26) ratios compared to the litter material used in our study with hardly any overlap in the range covered by the two sets of litter material. Nitrogen:P ratios above 15 to 22 are believed to indicate P rather than N limitation of decomposition (Aerts, 1997; Gusewell & Freeman, 2005; Smith, 2006). Based on these threshold values one would expect a strong P fertilization effect on the litter material used in our study and an eventually more important combined effect of N+P fertilization on the litter material used in Cleveland *et al.* (2006) study. However, just as total litter C is a poor indicator for the availability of C compounds to decomposers, the total N and P might not very well reflect the relative availability of these two nutrients. The underlying mechanisms for these contrasting results are presently not clear, and would need further experimental tests potentially with a gradient of N and P fertilization, different forms of N and P fertilizers and also with detailed analyses of microbial community composition in response to these different treatments.

Collectively, our results highlight that, while C-related trait (particularly condensed tannins) drive the variation in mass loss, the litter P status drive the extent of nutrient limitation by its own, and may probably have important consequences on nutrient immobilisation in this tropical rainforest.

Chapitre 3

Dissimilarité stoechiométrique dans les mélanges de litières

Litter mixture decomposition under C, N, and P fertilization in a tropical rainforest

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Introduction

A growing number of studies is showing that plant litter diversity alter decomposition and subsequent nutrient cycling (Gartner & Cardon, 2004; Hättenschwiler *et al.*, 2005). Decomposition in mixed litter species assemblages is often different than values predicted from single species, with synergistic mixture effects in the majority of cases (Gartner & Cardon, 2004). These positive mixing effects, however, show mostly no relationship with the number of litter species included in the mixture but depend on particular species included in the mixtures (Wardle *et al.*, 1997; Gessner *et al.*, 2010). A mechanistic understanding of species composition effects on litter mixture decomposition is key for the assessment of the impact of non-random plant species loss or plant species composition changes on decomposition. It appears that non-additive effects of mixed litter decomposition is mostly related to chemical differences between litter species (Epps *et al.*, 2007; Gessner *et al.*, 2010). For example, the combination of chemically different litter species may improve the energetic and nutritional balance for decomposers, leading to an overall increase of decomposer activity (Gessner *et al.*, 2010) or to a more diverse soil community, which will then results in a more efficient substrate use, through niche complementarity (Hooper *et al.*, 2000). Other litter chemistry related mechanisms discussed in the literature include nutrient transfer among litter species (McTiernan *et al.*, 1997; Schimel & Hättenschwiler, 2007) or modifications of the presence or feeding behaviour of detritivores (Hättenschwiler & Gasser, 2005; Swan & Palmer, 2006). While divergence of litter quality of component species should be the driver of both of these groups of mechanisms, the few existing studies using functional diversity approaches based on initial litter chemistry traits reported conflicting results (Hoorens *et al.*, 2003; Meier & Bowman, 2010; Barantal *et al.*, 2011). For example, Meir and Bowman (2010) provide a rather good explanation of non-additive effects on soil respiration and net N mineralization in litter mixtures of alpine herbaceous species using the Shannon index calculated from 9 chemical, mostly carbon-related litter traits. Other studies, however, did not find any relationships between non-additive litter mixture effects and initial chemical divergence among leaf litter species (Hoorens *et al.*, 2003; Barantal *et al.*, 2011). A better assessment of the site- and litter-specific

nutrient and energetic constraints on decomposers imposed through litter quality may improve the understanding of how and to what extent litter mixture effects operate on decomposition.

Forest tree leaf litter exhibits considerably higher C:nutrient ratios compared to decomposers (Daufresne & Loreau, 2001; Hessen *et al.*, 2004). This stoichiometric imbalance (mismatches between elemental ratios of consumers and their food) is expected to be important for the control of decomposition because food low in nutrients relative to carbon may impose severe growth constraints on decomposers (Sterner & Elser, 2002). In contrast to temperate forests where nitrogen (N) often limits decomposition (Carreiro *et al.*, 2000), many tropical rainforests grow on very old and highly weathered soils that are depleted in rock-derived nutrients and are considered to be principally phosphorus (P) limited (Walker & Syers, 1976; Vitousek & Sanford, 1986; Vitousek *et al.*, 2010). Accordingly, there is some evidence showing that soils microorganisms (Cleveland *et al.*, 2002), soil fauna (McGlynn *et al.*, 2007) and litter decomposition (Hobbie & Vitousek, 2000; Kaspari *et al.*, 2008) are P limited. However, decomposition is also often limited by poor C quality regardless of the type of ecosystem (Swift *et al.*, 1979; Hobbie, 2000). Poor C quality with low concentrations of labile C compounds and high concentrations of condensed tannins can effectively curb down decomposer activity and slow decomposition in the Amazonian rainforest of French Guiana (Coq *et al.*, 2010; Hättenschwiler *et al.*, 2011). This C-quality control seems to be even more important than nutrient control (Hättenschwiler & Bracht Jørgensen, 2010) despite the very low litter P concentrations measured in the leaf litter of this forest (Hättenschwiler *et al.*, 2008). The relative importance of C and nutrient control, however, was modulated by the presence of soil fauna that was more susceptible to both C quality and stoichiometric dissimilarity of litter mixtures than microorganisms alone (Hättenschwiler & Bracht Jørgensen, 2010). There is increasing recent evidence that soil fauna is particularly important for decomposition in tropical rainforests (Wall *et al.*, 2008; Coq *et al.*, 2010). The respective influences of nutrient and C limitation on decomposition in tropical rainforests were only little studied, and the role of soil fauna is particularly poorly documented. Apart of a better understanding of control factors over decomposition in these forests, a more detailed assessment of the relative importance of nutrient and C limitation may also allow to better

determine the underlying mechanisms of leaf litter mixture effects on decomposition. One way to that is by combining a litter mixing study with experimental fertilization with the key resources N, P and C. A recent litter decomposition study in a stream ecosystem showed that non-additive effects on litter mixture decomposition were suppressed with N enrichment (Rosemond *et al.*, 2010). They observed less variation in C: N ratios among litter species in response to N fertilization, suggesting that increased N availability reduced overall N limitation and diminished the potential of synergistic mixture effects due to resource complementarity and N-transfer among litter species in mixtures. To our knowledge a similar study combining litter mixing and fertilization does not exist in terrestrial systems, and the addition of C in particular has not yet been assessed.

In this study we combined the manipulation of litter stoichiometric diversity by using different litter mixtures with an experimental C, N, and P fertilization in the field of a tropical rainforest of French Guiana. We used six different litter types from tropical tree species that vary in initial C: N and N: P stoichiometry and composed litter mixtures in order to create a wide gradient of stoichiometric dissimilarity. We hypothesized that (1) Non-additive litter mixture effects on decomposition are related to the dissimilarity in leaf litter C: N and N: P stoichiometry with increasing non-additive effects with increasing stoichiometric dissimilarity, that (2) these non-additive mixture effects are less important or disappear with C, N, P fertilization, and that (3) litter-feeding soil fauna exacerbate the non-additive litter mixture effects and the C, N, P fertilization effects.

Material and methods

Study site and fertilization design

The experiment was carried out in an undisturbed Amazonian rainforest at the Paracou experimental station in French Guiana (5°18’ N, 52°53’ W). The site is characterized by a typical tropical wet climate with a long-term average annual temperature of 26 °C (1971-2001) and only little intra annual variation. The average annual precipitation is 3041 mm (1971-2001) and intra annual variations in precipitation are substantial with less rainfall during two rather dry periods in March and from mid-August to mid-November (Gourlet-Fleury S. *et al.*, 2004). The tree species richness is around 140 species ha^{-1} with a mean density

of 620 individual trees ha^{-1} (individuals of a diameter > 0.1 m at breast height) (Bonal *et al.*, 2008). Soils are classified as nutrient-poor acrisol (FAO 1998) in the top-soil developed over a Precambrian metamorphic formation called the Bonidoro series. Soil analyses at our study site showed a mean pH of 4.7 and a sandy soil texture with an average of 74% sand The average soil C content was 0.02 g C g^{-1} of dry soil, N content was 1.5 mg N g^{-1} of dry soil, and Olson-P content was 0.10 mg P g^{-1} dry soil (see Fanin *et al.*, 2011 for further details).

Within five blocks of natural forest, C, N and P fertilization was applied in all possible combinations. We included a control treatment (no fertilization) and an additional fertilization treatment where we added major cations (K, Ca, Mg) and micronutrients (S, B, Zn, Cu, Fe, Mo) yielding a total of nine treatment plots in each of the five blocks arranged in a randomized complete block design. Individual plots cover an area of 30.25 m^2 (5.5 m x 5.5 m) with at least 5 m distance between individual plots. The five blocks were established within a rather homogeneous zone on flat terrain to avoid lateral fertilizer losses by runoff. Blocks were separated among each other by 50 m to 300 m. Fertilizers were added in the form of cellulose for C (commercial susbtrate Waterspare, celliob industry, FRANCE), as coated urea ($[(NH_2)_2CO]$) for N, as $[KH_2PO_4]$ for P, and as HBO_2, $CuSO_4$, $FeSO_4$, $MnSO_4$, $ZnSO_4$, $(NH_4)_6Mo_7O_{24}$, K_2SO_4 and Ca-EDTA for micronutrients and major cations. These forms of nutrients are commonly used in large-scale fertilization experiments (Hobbie & Vitousek, 2000; Kaspari *et al.*, 2008). In order to determine the amount of fertilizer to be added we run a preliminary laboratory litter decomposition experiment using five different levels of C, N and P based on the average natural annual inputs of C, N and P via leaf litterfall in the studied forest (281g C m2 year-1, 6.5g N m2 year-1, 0.14g P m2 year-1 respectively, Bonal *et al.*, 2008; Hättenschwiler *et al.*, 2008) as the baseline. According to these preliminary tests, we chose a C addition equivalent to half of the total natural annual leaf litter C-input (1405 kg C ha^{-1} $year^{-1}$), a N fertilization equivalent to twice the natural annual leaf litter N input (130 kg N ha^{-1} $year^{-1}$),and a P fertilization equivalent to 50-fold the natural annual leaf litterP input (69 kg P ha^{-1} $year^{-1}$). Plots with micronutrient additions received a liquid micronutrient fertilizer equivalent to 22 kg ha^{-1} $year^{-1}$ consisting of H_3BO_3 (1150 ppm), $CuSO_4$ (1150 ppm), Fe-EDTA (2%), $MnSO_4$ (1150 ppm), $ZnSO_4$ (600 ppm) and $(NH_4)_2MoO_4$ (600 ppm), plus K_2SO_4 equivalent to 87 kg K ha^{-1} $year^{-1}$ and also Ca-EDTA corresponding at 50 kg Ca. ha^{-1} $year^{-1}$. These quantities of nutrient additions were largely comparable to other

fertilization experiments for example in montane tropical rainforests (Hobbie & Vitousek, 2000) or lowland tropical rainforests (Cleveland *et al.*, 2006; Kaspari *et al.*, 2008). Fertilizers were applied twice a year during the drier periods (from mid august to mid November and in March-April) in order to avoid initial nutrient leaching during the rainy seasons.

Plant material

Leaf litter from the 6 tree species *Carapa procera, Goupia glabra, Hymenaea courbaril, Platonia insignis, Simarouba amara,* and *Vochysia tomentosa* were chosen for their wide variation in C:N, C:P, and N:P stoichiometries (see Barantal *et al.,* manuscrit 1). Freshly fallen leaf litter of each species was collected in a tree plantation adjacent to the natural rainforest. This plantation was set up by the French research centre CIRAD in 1983 (Coopération Internationale en Recherche Agronomique pour le Développement) and consists of closed canopy mono-specific stands of a total of 16 tree species including the six species used in this study (see Roy *et al.*, 2005 for more details). Leaf litter of each of the six species was collected in litter traps suspended in each stand (covering a total area of roughly 25 m^2 to have a representative sampling at the stand level) emptied twice a month during the year 2009. Leaf litter was air dried immediately upon collection in the field, pooled across sampling dates and stored dry. The litter from each species pool was sorted, and only intact leaves without signs of herbivory, galls or fungal attack or with atypical texture or color were retained for the experiment. Litter quality from these six species has been described in detail by Coq *et al.* (2010) and Barantal *et al.* (manuscript 1).

Litter mixture decomposition experiment

Litter mixtures were constituted from the six above mentioned litter species and comprised mixtures of 2, 3, 4 and all 6 species in addition to all mono-specific litter treatments. Species composition in mixtures was determined to maximize stoichiometric dissimilarity and by respecting an equal representation of each litter species within each level of litter species richness (each species was present exactly in two 2-species, two 3-species, and two 4-species mixtures and in the single 6-species mixture. The stoichiometric dissimilarity index was computed using the Rao's quadratic entropy, (Botta-Dukat, 2005;

Epps *et al.,* 2007) integrating the average pair-wise distances between *n* component species of mixtures as well as species relative abundances computed as follows:

$$Rao_{ij} = \sum_{i=1}^{n} \sum_{j=1}^{n} \rho_i \rho_j d_{ij}$$

where ϱ_i and ϱ_j are the relative abundance by biomass of species i and j, respectively, and d_{ij}, the stoichiometric dissimilarity coefficient based on Euclidean distance between two species i and j. Euclidean distances were calculated from the C:N and N:P ratios of all possible combinations of the six species. We retained those species combinations allowing a maximum breath of stoichiometric indices while respecting the criteria of having each species only twice in mixtures at any richness level (once for the 6-species mixture). This yielded a total of 14 different litter mixtures (six 2-species, four 3-species, three 4-species and one 6-species mixtures).

Two different types of 0.15 x 0.15 m litterbags were constructed in order to allow or not the access of macrofauna. Mesh bags of 68 mm (68PES4/135, DIATEX) were used to exclude all meso- and macrofauna, and 8 mm mesh bags (F.1004, DIATEX, St-Genis-Laval, France) were used to allow fauna access. To avoid losses of litter fragments through the largest mesh width during field exposure, the soil surface facing side of the litterbag was made of 0.5 mm mesh. Each litterbag was filled with 8 g of air-dried litter, with mixtures containing equal mass proportions of the component species. One of each of the total forty different litter bag types ((6 single species + 14 mixtures) x 2 mesh sizes) were placed randomly in each of the 45 field plots described above, yielding a total of 1800 litter bags deployed from 3 to 11 September 2009, one month before the second event of fertilization.

All litterbags were retrieved after a total of 156 days of field exposure from 9 February to 17 February 2010 in the same order as they have been placed in the field. Upon harvest, remaining litter was gently rinsed with tap water to remove adhering plant root parts, invertebrates and soil particles, dried at 65°C to constant weight and weighed to determine remaining litter mass.

Data Analysis

Litter mass loss is expressed in percent of initial litter dry weight (oven-dry weight was determined from sub-samples of the initial air dried litter pool). Expected mass loss (E) of litter mixtures was estimated as the mean mass loss of the component species decomposing in isolation in the corresponding fertilizer and fauna treatments. The calculation of E was based on the average of the 5 replicates (blocks) in order to have a robust estimate of E. According to Wardle *et al.* (1997), the relative mixture effect was calculated as the ratio ((observed – expected) / expected) mass loss for each mixture. If the relative mixture effect differs from zero, it indicates non-additive litter mixture effects on decomposition. A negative and positive deviation from zero is called antagonistic and synergistic effect, respectively.

Paired t-tests were used to test if observed mass loss differed from expected mass loss. Overall relative mixture effects were tested against zero with one-sample t-tests. Likewise, we used one-sample t-tests to test whether overall antagonistic and synergistic effects (all relative mixture effects lower or higher than zero pooled separately) were significantly different from zero. We used a linear mixed model to test for effects of fertilization (all fertilizer treatments included as individual levels of this factor), fauna presence/absence and species composition (all fixed factors) and for block effects (random factor) on relative mixture effects. To investigate the effects of litter species presence within mixtures and of C, N, and P fertilization in more detail, we used linear mixed models with the presence/absence of each species in mixtures, the presence of C, N, and P fertilizer (fixed factors) and block (random factor) on each of the two mesh sizes of litter bags separately. In this analysis the micronutrient fertilizer treatment was excluded to respect a fully factorial design. The two- and three-way interactions between C, N and P supply were allowed but only two-way interactions between species presence/absence and C, N, or P fertilizer application were included. If theses interactions were not significant ($P > 0.05$), they were removed from the model and the analysis was run again. Tukey post hoc tests were used to explore multiple comparisons of interaction terms more specifically. Litter mass loss data were log transformed before analyses to alleviate heteroscedasticity and improve normality.

Relationships between stoichiometric dissimilarity and the relative mixture effects were explored with linear regression analyses. Mixtures responses to resource supply, *i.e* the

net fertilization effect on relative mixture effects across the different mixtures, were calculated as the difference between the relative mixture effects in fertilized treatments minus the relative mixture effects in control treatments within each block. Linear regression between these net fertilization effect and stoichiometric dissimilarity were explored for each resource supply treatments. The R package (version 2.4.0; R Development Core Package 2006) was used for statistical analyses.

Results

Across the entire data set, the observed litter mixture mass loss deviated from predicted mass loss calculated from the component species decomposing individually (Fig. 1, paired t-test between observed and expected mass loss: t_{1257} = 23.2***). Relative litter mixture effects ranged from clearly negative effects (- 9.8%) to strongly positive effects (+ 50.1%). Synergistic effects were stronger and more frequent (83.3% litter mixtures decomposed more rapidly than predicted) than antagonistic effects. However, relative mixture effects depended on the presence of fauna, species composition in litter mixtures and fertilization (Table 1). The significant interactions between (i) fauna and litter species composition, and (ii) fauna and fertilization (Table 1) indicate that fauna activity was important in influencing the effects of species composition and fertilization on the relative mixture effects. A substantial amount of variation in relative mixture effects could also be allocated to the block effect, as revealed by comparing the obtained linear model without random block effect against the full mixed model (p-value < 0.0001). Relative mixture effects were entirely driven by species composition and not by species richness (Fig.2). When replacing the species composition term with species richness in the full model, there was no longer an effect on the relative mixture effect.

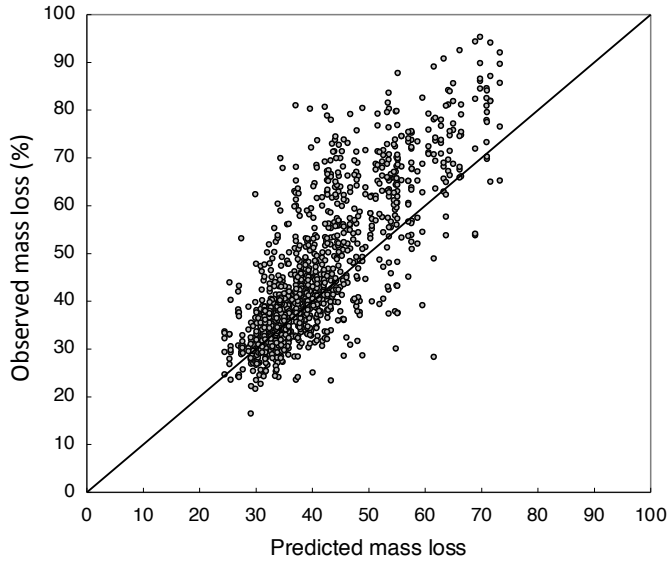

Figure 1: Observed mass loss of litter mixtures following predicted mass loss (based on average mass loss of single components species) across all data set from a multifactorial experiment (litter diversity, external resource supply and absence/presence of fauna manipulation) in an Amazonian rainforest. The 1:1 line indicates that observed and predicted values are similar. Each point represents an individual litterbag.

Table 1: Linear mixed model to test the effects of presence/absence fauna (F), species composition of mixtures (S) and resource supply (R, all resource treatments included) and their interactions, on relative mixture effects.

	df	F-value	p-value
Fauna (F)	1	269.9	<0.0001
Species composition (S)	13	2	0.02
Resource supply (R)	8	4	0.0001
F * S	13	1.9	0.024
F * R	8	2.2	0.024
S * R	104	0.7	0.1
F * S * R	104	1.1	0.26

Fauna and species composition

Based on F-ratios, fauna had by far the strongest influence on the relative mixture effects (Table 1 fauna effect: F = 269.9 ***). Fauna presence resulted in a strong overall increase in relative mixture effects, leading to an average 4.2 fold higher relative mixture effect as compared to when fauna was excluded (Fig 2). With fauna the relative mixture effects ranged from -8.5% to 50.1% (16.8% on average) compared to -9.8% to 28.9% (4% on average) without fauna (Fig 2). Only three litter mixtures decomposed slower than predicted with fauna, whereas 31% of all mixtures decomposed slower than predicted without fauna, resulting in a mean antagonistic effect that was significantly lower than zero (t_{193} = -5.1*** considering all mixtures showing antagonistic effects). Synergistic effects (all mixtures showing a mean relative mixture effect higher than zero) were on average significantly greater than zero, both with (mean = 17.3%, t_{613} = 16.9***) and without fauna (mean = 7.5 %, t_{434} = 11.0***).

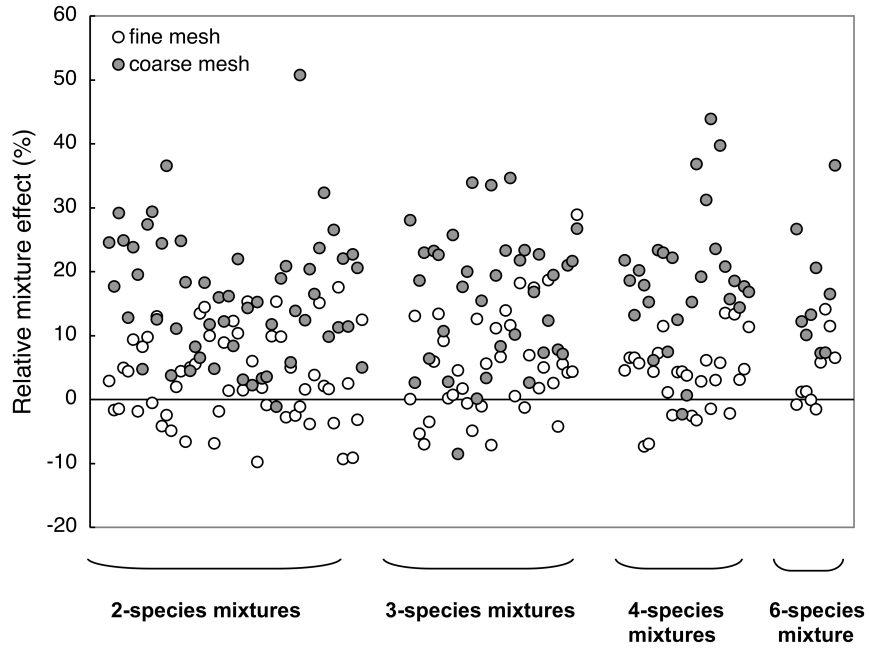

Figure 2: Relative mixture effects ((observed mass loss – predicted mass loss) / predicted mass loss x 100) ranged by species richness in mixtures (varying to 2 from 6 litter species). Grey symbols indicate data in the presence of fauna (corresponding to coarse mesh bags) and blanck symbols data in the absence of fauna (corresponding to fine mesh bags). N=5.

A closer look at the litter species composition effect, using linear mixed models to test for the effects of the presence of particular species, revealed that the relative mixture effect was mostly driven by some particular litter species (Table 2). In the presence of fauna, litter of *Hymenea* and *Simarouba* slightly but significantly increased the overall mixture effects by 3.2% and 1.8%, respectively. The presence of *Platonia* litter also marginally increased the relative mixture effects. Without fauna, litter of *Carapa* showed the strongest influence on relative mixture effects (Table 2, F = 12.71***), resulting in lower relative mixture effects (2.4% on average) compared to mixtures that did not contain *Carapa* litter (6.2% on average). In contrast, the presence of *Goupia* litter within mixtures increased relative mixture effects (Table 2, F = 6.98**), from an average of 2.3% without *Goupia* to an average of 6.2% when *Goupia* was included.

Table 2: Linear mixed models to test for the effects of the presence of each litter species and of the occurrence of C. N or P supply (micronutrient excluded) on relative mixture effects within each mesh size bags. Fine mesh bags excluded meso- and macrofauna whereas coarse mesh bags allowed meso- and macrofauna access.

	Df	F-value	P-value		Df	F-value	P-value
Without fauna				***With fauna***			
Carapa	1	12.71	0.0004	*Carapa*	1	0	0.99
Goupia	1	6.98	0.0085	*Goupia*	1	0.28	0.6
Hymenea	1	1.74	0.19	*Hymenea*	1	9.05	0.0028
Platonia	1	0.55	0.46	*Platonia*	1	3.47	0.063
Simarouba	1	0.68	0.41	*Simarouba*	1	6.36	0.012
Vochysia	1	1	0.32	*Vochysia*	1	0.18	0.68
C	1	0.09	0.76	C	1	9.3	0.0024
N	1	11.7	0.00068	N	1	7.45	0.0066
P	1	0.72	0.4	P	1	0.01	0.94
C:N	1	13.08	0.00033	Platonia:C	1	7.55	0.0062
N:P	1	6.49	0.011	Platonia:P	1	5.18	0.023
Hym:C	1	7.24	0.0074	Simarouba:C	1	4.02	0.045

Note: An initial linear mixed model was computed including all interactions among C. N. P supply and second order interactions between species and each resource (C or N or P). Only interactions that accounted for significant variation in relative mixture effects were further retained.

Impact of resource supply on relative mixture effects

The effects of C, N and P fertilization were explored within each mesh size (Table 2). In the control treatment (without any fertilization), the average relative mixture effects were 10.4% and 18.2% without and with fauna access, respectively. The smallest and highest average relative mixture effect with any type of fertilization was -3.4% and + 5.2% without fauna compared to + 11.2% and + 23.7% with fauna.

When fauna did not have access to decomposing litter, only N fertilization significantly altered relative mixture effects (F = 11.7***, Table 2), with less relative mixture effects than in control treatments (Fig. 3). Moreover, N fertilization shifted the average relative mixture effect to clearly antagonistic effects (-3.35% on average) that were significantly lower than zero (t_{69} = -2.9**). These negative N fertilization effects were somewhat counteracted by an additional fertilization with P or C (significant interaction term of N with P and C fertilization, Table 2).

The negative impact of N fertilization on the relative mixture effects persisted when soil fauna had access to the litterbags. The mean relative mixture effect decreased from 18.4% without N fertilization to 14.9% across all N-fertilized plots (Table 2, Fig 3). Similarly, P fertilization did not influence the relative mixture effects as was observed without fauna. However, P fertilization interactively influenced the relative mixture effect in presence of *Platonia* litter when soil fauna had access to decomposing litter (Table 2). Relative mixture effects tended to be higher in presence of *Platonia* without P fertilization, but this *Platonia* effect disappeared when mineral P was added. In presence of fauna, C fertilization significantly, but relatively weakly increased the relative mixture effect (16% without C fertilization compared to 17.9% with C fertilization, F = 9.3**, Table 2, Fig 3). However, the effect of C fertilization was interactively influenced by the presence of *Platonia* and *Simarouba* leaf litter (Table 2). The response to C fertilization was substantially higher in absence of *Platonia* (12.3 % without C to 20.4% with C) or in presence of *Simarouba* (from 15.3% without C to 20% with C). Finally, fertilization with only micronutrients decreased the relative mixture effect without fauna (from 10.3% in the control treatment to 2.2% with added

micronutrients, paired t-test: t_{69}=3.5***), but had no effect when fauna was included (18.2% in the control treatment and 17.9% with added micronutrients).

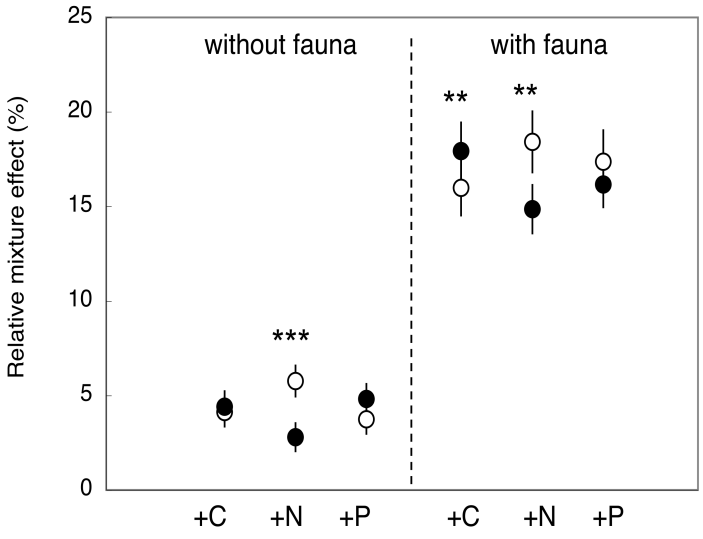

Figure 3: Relative mixture effects from the factorial-CNP fertilization experiment without and with fauna (mean ± SE). Relative mixture effect was calculated as (observed mass loss − expected mass loss) / expected mass loss x 100. Dark circles represent data for litterbags in plots receiving C, N, or P; white circles in the plots failing to receive C, N, or P respectively. Stars denote differences in relative mixture effects between litterbags receiving and not receiving a given supply: **Significance at p-value < 0.01 and ***Signifiance at p-value< 0.001. N = 280.

Does stoichiometric dissimilarity explain relative mixtures effects and their response to fertilization?

Without fauna, the relative mixture effects did not correlate with stoichiometric dissimilarity of litter mixtures, regardless of the fertilization treatment (data not shown). However, in presence of fauna, relative mixture effects showed a trend to increase with stoichiometric dissimilarity in the control treatment (r^2 = 0.25, P = 0.066, Fig 4a). Interestingly, this positive correlation between relative mixture effects and stoichiometric dissimilarity disappeared with added fertilizer. When we plotted the net effect of fertilization on the mixture effects as a function of stoichiometric dissimilarity, a consistent decreasing pattern was found for the combined fertilization with N + P, C + P and C + N + P fertilization (Fig 4b, r^2 = 0.33*, r^2 = 0.38*, r^2 = 0.29* for N+P, C+P and C+N+P treatments, respectively).

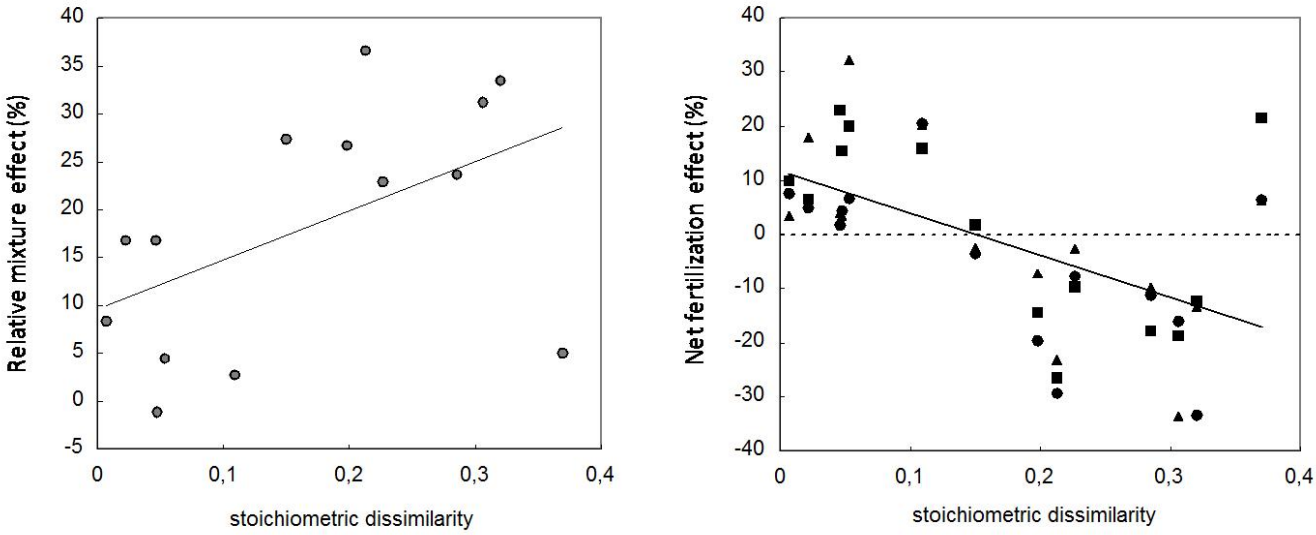

Figure 4 a) Mean relative mixture effect across the different mixtures with fauna access in control treatment following stoichiometric dissimilarity in mixtures; and b) net fertilization effect across the different mixtures with fauna access following stoichiometric dissimilarity in mixtures; circles represent the net NP effect, triangles represent the net CP effect and squares the net CNP effect. The regression line corresponds to the linear regression over data from the 3 resource treatments. Stoichiometric dissimilarity were calculated from initial leaf litter C:N and N:P ratios of single species components in mixtures. The net fertilization effect was calculated for each mixture as the mean relative mixture effect in fertilized plots minus the mean relative mixture effect in the control treatment (without resource supply). A negative fertilization effect indicates a more negative or less positive mixture effect in the fertilized plots than in the control plots.

Discussion

Here we exposed a large number of different litter mixtures and the respective single litter treatments to all combinations of C, N, and P fertilization in a neotropical rainforest in order to study to what extent stoichiometric dissimilarity of litter mixtures determine non-additive mixture effects on decomposition and how they are influenced by external resource availability. With the large data set presented here, we found that more than 80% of all litter mixtures of several species of leaf litter decomposed faster with up to 50% higher mass loss than predicted and with a significant average stimulation of 10.4%. The relative mixture effect did not vary with the number of species included in the mixture according to previous studies that have concluded that species composition and thus the specific litter traits involved are more important than species richness in driving non-additive responses (Lecerf

et al., 2007; Warnecke *et al.*, 2007; Ball *et al.*, 2008; Jonsson & Wardle, 2008; Hättenschwiler & Bracht Jørgensen, 2010; Barantal *et al.*, 2011).

The pronounced poverty in soil P and the still surprisingly high variation in litter P concentrations among co-occurring tree species at our study site (Hättenschwiler *et al.*, 2008) suggested litter P and its relative abundance compared to the other key elements C and N as a particular important litter trait for decomposers and subsequent decomposition. In Costa Rican tropical forests litter fauna abundance decreased significantly with increasing soil C: P ratio (McGlynn *et al.*, 2007) and microbial activity responded positively to experimental P fertilization (Cleveland *et al.*, 2002; Cleveland & Townsend, 2006). We expected that a higher heterogeneity in litter species-specific P concentrations of litter species contributing to litter mixtures would have a greater potential for synergistic mixture effects. Accordingly, we stated in our first hypothesis that non-additive litter mixture effects increase with increasing stoichiometric dissimilarity. In line with our hypothesis, relative mixture effects were positively correlated with stoichiometric dissimilarity, but only when fauna was present. This decomposer food web dependent effect of litter mixture stoichiometry could indicate that litter detritivores are better capable to exploit diverse food sources at the spatial scale of litter mixtures than microorganisms.

Our second hypothesis stated that fertilization would lead to diminished mixture effects by homogenizing variation in substrate quality among litter species or simply by providing an alternative litter-independent source of mineral nutrients and energy. We partly confirm our hypothesis with respect to nutrients, while C fertilization tended to increase relative mixture effects when fauna had access. Nitrogen fertilization reduced mixture effects regardless of fauna presence. Moreover, relative mixture effects shifted from an average synergistic mixture effect without N fertilization to an antagonistic litter mixture effect. The effect of P fertilization on the relative mixture effects was much smaller than that of N fertilization. It showed also a trend for decreased relative mixture effects, but only in presence of fauna. Our results are broadly comparable with the only other study assessing the effect of fertilization on litter mixture effects in a temperate stream ecosystem (Rosemond *et al.*, 2010). They also showed that mixture effects were suppressed by elevated streamwater. Rosemond *et al.* (2010) also measured C and N concentration of remaining leaf litter at the

end of the experiment and found that N fertilization increased N concentration of all litter species and reduced interspecific variation in C: N ratio. In our study we did not measure final litter nutrient concentration, but we found a negative correlation between the net fertilizer effects of the combined additions of C+N+P, C+P and N+P and initial litter stoichiometric dissimilariy when fauna was present. This result strongly supports the evidence that initial variation in stoichiometry among leaf litter species in mixture mediate the relative mixture effects in presence of fauna.

Among all the driving variables assessed here, the presence of fauna had the strongest impact on litter mixture effects. Fauna contributed to an increasing synergistic effect that showed an average of 4% without fauna, and an average of 16.8% in presence of fauna. The key role of soil fauna for decomposition at our study site has been documented previously (Coq *et al.*, 2010; Hättenschwiler *et al.*, 2011) and is generally in line with the idea that fauna contribute comparatively more to decomposition in tropical ecosystems than in ecosystems at higher latitudes (Lavelle *et al.*, 1993; Gonzalez & Seastedt, 2001; Wall *et al.*, 2008; Yang & Chen, 2009). The contribution of soil fauna to litter mixture decomposition is rarely considered, but the few extra-tropical studies that have specifically tested for soil fauna effects found that non-additive effects on litter mixture decomposition were mostly attributed to the presence of detritivores (Hättenschwiler & Gasser, 2005; Schadler & Brandl, 2005; De Oliveira *et al.*, 2010; Giesselmann *et al.*, 2010; Vos *et al.*, 2011). Furthermore, studies that manipulated both litter diversity and macrofauna diversity have shown that macro-detritivore diversity also play a critical role on litter mixture effects (Hättenschwiler & Gasser, 2005; De Oliveira *et al.*, 2010).

Chapitre 4

Diversité chimique et histoire du sol

Long-term presence of tree species but not chemical diversity affect litter mixture effects on decomposition in a neotropical rainforest.

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Abstract

Plant litter diversity effects on decomposition rates are frequently reported, but with a strong bias towards temperate ecosystems. Altered decomposition and nutrient recycling with changing litter diversity may be particularly important in tree species rich tropical rainforests on nutrient-poor soils. Using 28 different mixtures of leaf litter from 16 Amazonian rainforest tree species, we tested the hypothesis that litter mixture effects on decomposition increase with increasing functional litter diversity. Litter mixtures and all single litter species were exposed in the field for 9 months using custom-made microcosms with soil fauna access. In order to test the hypothesis that the long-term presence of tree species contributing to the litter mixtures increases mixture effects on decomposition, microcosms were installed in a plantation at sites including the respective tree species composition and in a nearby natural forest where these tree species are absent. We found that mixture decomposition deviated from predictions based on single species, with predominantly synergistic effects. Functional litter diversity, defined as either richness, evenness, or divergence based on a wide range of chemical traits, did not explain the observed litter mixture effects. However, synergistic effects in litter mixtures increased with the long-term presence of tree species contributing to these mixtures as the home-field advantage hypothesis assumes. Our data suggest that complementarity effects on mixed litter decomposition may emerge through long-term interactions between aboveground and belowground biota.

Key words: Amazonian rainforest, chemical diversity, decomposition, functional diversity indices, litter traits.

Introduction

Tropical forests are among the biologically most diverse and ecologically complex ecosystems and play a crucial role in the global carbon cycle and climate system (Bazzaz, 1998; Dirzo & Raven, 2003). Heavily impacted by human activities, tropical forests undergo rapid changes in particular due to extensive deforestation (Achard *et al.,* 2002; Mayaux *et al.*, 2005) predicted to result in pronounced biodiversity loss (Turner, 1996; Bazzaz, 1998; Laurance, 2007). Species loss and changes in species composition will likely affect ecosystem processes such as net primary productivity and carbon cycling (Chapin *et al.,* 2000; Loreau *et al.*, 2001). Based on a series of simulations of non-random tree species losses in the tropical rainforest of Panama, Bunker *et al.* (2005) suggested that the storage of aboveground carbon could vary by more than 600% depending on the species loss scenarios.

While important conceptual advancements and acquisition of empirical data over the last decade allow a better understanding of the relationships between biodiversity and plant growth and productivity (Hooper *et al.,* 2005; Marquard *et al.,* 2009), the impact of changing biodiversity on other ecosystem processes such as decomposition and nutrient cycling lag behind (Hättenschwiler *et al.,* 2005; Gessner *et al.,* 2010). Decomposition is a critical determinant of the global carbon cycle and nutrient turnover (Swift *et al.,* 1979; Del Grosso *et al.*, 2005; Parton *et al.,* 2007). Recycling of nutrients constitutes a particularly important nutrient source for organisms in old and weathered soils that are highly nutrient depleted like in many tropical ecosystems (Walker & Syers, 1976; Crews *et al.,* 1995; Vitousek *et al.,* 2010). The high tree species diversity and typically low abundance of individual species of tropical rainforests have recently been reported to result in a chemically highly diverse litter input at small local scales (Hättenschwiler *et al.,* 2008) and associated species-specific decomposition rates (Coq *et al.,* 2010). Such high chemical diversity of leaf litter input may be a key factor to understand why litter mixture decomposition deviates from predictions based on single species decomposition as it is frequently observed in studies from predominantly temperate ecosystems (Wardle *et al.*, 1997; Gartner & Cardon, 2004).

Potential mechanisms of litter diversity effects on decomposition include nutrient transfer between litter types (Schimel & Hättenschwiler, 2007), resource complementarity (Gessner *et al.*, 2010), changes in stimulation or suppression of microorganisms (Bardgett & Shine, 1999), and modifications of the presence or feeding behaviour of detritivores (Hättenschwiler & Gasser, 2005; Swan & Palmer, 2006). All these mechanisms are intimately related to the quality of litter types included in the mixture. Recently, Epps *et al.* (2007) proposed a theoretical framework for using litter chemical parameters as functional traits and explicitly accounting for chemical heterogeneity in litter mixtures. Chemical diversity indices based on multiple chemical traits might allow predicting litter mixture effects on decomposition. Although the potential of functional approaches to better understand and predict biodiversity effects on ecosystem functioning is widely recognised (Diaz & Cabido,

2001; Hooper *et al.*, 2005), the definition and mathematical formulation of functional diversity is a complex task (Petchey & Gaston, 2006). Rather than using one single index, several indices focussing on different aspects of functional diversity such as functional richness, evenness and divergence yield complementary information and should be used in concert (Mason *et al.*, 2005; Villeger *et al.*, 2008).

Here we attempted to test the predictive power of litter chemical diversity on decomposition of 28 different litter mixtures created from a pool of litter of 16 tree species from an Amazonian rainforest. These litter mixtures were not defined randomly, but represented existing long-term mixed litter inputs at intersections of planted monocultures in French Guiana (Roy *et al.*, 2005). With the simultaneous exposure of litter mixtures at the site of origin and in a nearby natural forest where the target species were not present, we aimed also to address the question whether the long-term adaptation of the decomposer community to a given litter mixture input from the tree canopy contributes to litter mixture effects. Multitrophic processes such as decomposition can result from evolutionary contingencies between plant species and belowground food webs (Gessner *et al.*, 2010). Plant species might exert selective pressure on decomposer communities via long-term litter input leading to decomposer communities adapted to particular litter types and hence a faster decomposition, also known as the "home field advantage (HFA)"(Hunt *et al.*, 1988; Vivanco & Austin, 2008; Ayres *et al.*, 2009). We hypothesized that (i) mixture decomposition and more specifically non-additive effects of litter mixtures increase with increasing functional (litter chemistry) diversity of mixtures and that (ii) the HFA leads to greater non-additive effects of litter mixtures at sites with a long-term input of the litter types included in the mixture than at sites without such long-term litter input of target species.

Materiel and methods

Study site

The experiment was conducted at the Paracou experimental station in French Guiana (5°18' N, 52°53' W) in a 25-year-old experimental plantation and in adjacent natural rainforest. The site is characterized by a typical tropical wet climate with a long-term average annual temperature of 26 °C (1971-2001) and an average annual precipitation of 3,041 mm (1971-2001). Temperature varies only little over the course of the year, but variations in precipitation are substantial with less rainfall during two rather dry periods in March and from mid-August to mid-November (Gourlet-Fleury *et al.*, 2004).

The plantation was established in 1984 within a natural forest by the French Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD). Twenty-four tree species chosen for their potential timber value and their abundance in rainforests of French Guiana were planted as monocultures (20 m x 20 m plots each) from

three-year-old seedlings (see Roy *et al.*, 2005 for more details). Some tree species did not establish well and our study focused on the 16 mono-specific plots that formed a closed canopy. The adjacent natural forest is characterized by a tree species richness of about 140 species ha^{-1} with a mean density of 620 individual trees ha^{-1} (individuals of a diameter > 0.1 m at breast height) (Bonal *et al.*, 2008). Soils are nutrient-poor acrisol (FAO 1998) developed on a Precambrian metamorphic formation called the Bonidoro series. Soil characteristics are broadly the same in the plantation (Roy *et al.*, 2005; Bréchet *et al.*, 2009) and the natural forest (Hättenschwiler & Bracht Jørgensen 2010) with a similar texture, and similar concentrations of carbon (16.2 and 18.7 g C/kg in the plantation and the natural forest, respectively), nitrogen (1 and 1.2 g N/kg), and phosphorus (0.006 and 0.0055 g "Olson P"/kg). The tree canopy in the plantation is somewhat more open (mean leaf area index of about 4, Roy *et al.*, 2005) than in the natural forest (leaf area index of about 6, Handa *et al.*, unpublished data).

Plant material and experimental design

Leaf litter from 16 tree species encompassing 9 families (see Appendix for species names and families) planted in the above-mentioned plantations was used. Freshly fallen litter was collected twice a month between February 2005 and December 2005 using three litter traps installed in each mono-specific plot. Leaf litter was air dried immediately upon collection in the field, pooled across sampling dates and stored dry. The litter from each individual species was homogenized, and only intact leaves without signs of herbivory, galls or fungal attack, atypical texture or color were chosen for the experiment. Chemical composition of the litter of all tree species is described in Coq *et al.* (2010). Tree species vary widely in leaf litter chemistry, with particularly large differences in the concentration of condensed tannins (from 0.1 to 3.5 % of dry mass), hemicelluloses (from 6.8 % to 27.8 % of dry mass) and phosphorus (from 0.016 to 0.056 % of dry mass) (Coq *et al.*, 2010; see Appendix for chemical description of species-specific leaf litter).

Litter mixtures were composed from the litter of the 16 tree species. In order to test the influence of long-term input and presence of litter of particular species on decomposition, litter assemblages were chosen to correspond to the naturally occurring mixtures at the mono-specific plot interfaces in the plantation. The plantation is organized following two adjoining rows of 12 contiguous plots each (see Roy *et al.*, 2005). Inter-plot zones allow natural combinations of two (at mid-width of the contiguous sides of the plots), four (at the contiguous corners of the plots) or three (at the corners in the cases when one of the initially planted species did not establish) species in the litter layer. The plantation layout yielded a total of 16 mono-specific litter treatments (from the 16 well-established tree species with a closed canopy), 16 two-species mixtures, 4 three-species mixtures, and 2 four-species mixtures. In order to include a higher number of three and four-species mixtures, we created additional mixtures by removing or adding a randomly chosen species to the existing four-

and three-species litter mixtures, respectively. In total, the experimental design included six different three- and four-species mixtures each (see Appendix for species composition of mixtures).

Custom-made field microcosms were used for the assessment of decomposition, with a diameter and height of 15 cm constructed from plastic cylinders. The bottom was left open to allow all soil fauna access and hyphal growth. Two 5 x 15 cm large openings were pierced on the sides and covered with 1 cm nylon mesh to avoid loss of litter or contamination of naturally occurring litter, but to allow soil macrofauna free access (the openings were at the level of the soil surface). To cover the top of the microcosms, we used a smaller mesh of 0.05 cm, in order to avoid contamination with small litter particles dropping from the canopy. Microcosms were placed on bare soil (natural litter layer was previously removed) and slightly inserted between 0.5 and 1 cm into the top soil with a distance of about 1m between individual microcosms. The natural litter at the spot was then evenly distributed around the microcosms to provide a continuous litter layer. Microcosms rather than litterbags were used for three reasons. They ensure a complete isolation of target litter substrates from surrounding natural litter, they do not alter the three dimensional structure of the litter layer (the flattened litter within litterbags would affect access and movement of litter fauna and microclimatic conditions), and they allow intimate contact with the soil surface. Each microcosm was filled with 10 g of air-dried leaf litter, with mixtures containing equal proportions of dry mass of the component species. Sub-samples of litter from each species were retained to determine the air- to oven-dry mass ratio.

The field microcosms were placed either close to the centre of the mono-specific tree plots (for the corresponding mono-specific litter treatments) or at the plot intersections (for the respective litter mixture treatments). Microcosms containing the same 16 mono-specific litter treatments and the same litter mixtures as those used in the plantation, were additionally exposed in adjacent natural rainforest. The location in the natural forest was chosen so that none of the 16 tree species used for the test were locally present, and thus without their long-term influence on the forest floor and soil. All 44 litter treatments (the 16 single species and 28 mixtures treatments) were replicated four times with two replicates per site (plantation and natural forest) yielding a total of 176 field microcosms. According to the patch-scale process of litter decomposition, individual microcosms were considered as independent replicates just as in most litterbag studies. Moreover, previous studies in the plantation (Bréchet *et al.*, 2009) and in the nearby natural forest (Hättenschwiler & Bracht Jørgensen, 2010; Fanin *et al.*, 2011) showed substantial variation in soil processes and decomposition at very small spatial scales that was as large or larger within blocks at the meter scale than among blocks of hundreds of meters distance (Fanin *et al.*, 2011) .

The litter was placed in the field on 10 February 2006 and removed on 10 November 2006 after a total of 273 days of exposure. The remaining litter was washed carefully to

remove adhering soil particles, roots, and fauna. All mixtures were separated into component species in order to assess species-specific litter mass loss. Given the coloration, morphological and structural differences, and patterns of leaf veins among species, litter species identification was possible. Unidentified litter material, when present, accounted for less than 3 % of total litter mass remaining and was attributed in equal quantities to each of the species represented in the mixture. Litter was then oven-dried (65 °C for 48 hours) and weighed to determine the remaining leaf dry mass.

Calculations and statistical analysis

Litter mass loss is expressed in percentage of initial litter oven-dry weight. Expected mass loss (E) of litter mixtures was estimated as the mean mass loss of the component species decomposing in isolation in the site-specific replicates. According to Wardle *et al.* (1997), the relative mixture effect was calculated as the ratio ((observed – expected) / expected) * 100 mass loss for each mixture. If the relative mixture effect differs from zero, it indicates non-additive litter mixture effects on decomposition. Negative and positive deviations from zero are referred to antagonistic and synergistic effects, respectively. Relative individual performance of individual litter species within mixtures is defined as the difference between observed mass loss in mixtures and observed mass loss in isolation divided by mass loss in isolation and multiplied by 100. The net site effect was calculated for each mixture as the mean of relative mixture effect in the plantation minus the mean of relative mixture effect in the natural forest. This net site effect was also calculated for each individual litter species within mixtures in the same way.

The chemical composition of mixtures was calculated as the average of the relative contribution of each species-specific chemical trait (see Appendix for chemical composition of mixtures). Beyond the average chemical composition of mixtures, the species-specific chemical traits were also used to characterize the functional diversity of litter mixtures using three different indices available from the literature. Because we used a total of eight different litter chemistry traits with a maximum of four species represented in mixtures, we chose the multivariate indices that can be calculated with a species number lower than trait number. As litter traits, we used the concentrations of nitrogen, phosphorus, lignin, cellulose, hemicellulose, condensed tannins, and soluble and total phenolics (Coq *et al.*, 2010). The functional diversity index (abbreviated as FD) proposed by Petchey and Gaston (2002), was chosen to represent functional richness (i.e. how much of the functional niche space is filled by the species). The computation of FD is based on the sum of lengths on hierarchical classifications and we used Euclidean distance and the un-weighed pair-group method using the arithmetic averages (UPGMA) clustering method. To describe functional divergence, we used the Rao's quadratic entropy, (Botta-Dukat, 2005; Epps *et al.*, 2007) integrating the

average pair-wise distances between *n* component species of mixtures as well as species relative abundances computed as follows:

$$Rao_{ij} = \sum_{i=1}^{n} \sum_{j=1}^{n} \rho_i \rho_j d_{ij}$$

where ρ_i and ρ_j are the relative abundance by biomass of species i and j, respectively, and d_{ij}, the dissimilarity coefficient based on Euclidean distance between two species i and j in the multivariate functional trait space. This index reflects how abundance is distributed within the volume of functional trait space occupied by a given species mixture. In order to capture another facet of functional diversity beyond differences among species, we used the Shannon index (H'_C) as modified by Meier and Bowman (2008) as follows:

$$H'_C = -\sum_{i=1}^{C} \rho_i \log \rho_i$$

where C is the total number of chemical traits and ρ_i is the proportion of the total mixture dry weight for the trait i. H'_C accounts for the presence and abundance of compounds (C forms, N, P), but as all compounds are present, H'_C represents the "evenness" or distribution of chemical traits. In the calculation of FD and Rao index, absolute values of traits can lead to a biased contribution of some traits that have numerically larger numbers; consequently all trait values were transformed by the standard deviation resulting in a mean of zero and a variance of one. No standardisation was applied in the calculation of H'_C since it already includes a logarithmic transformation.

Student t-tests were used to test whether antagonistic and synergistic effects in mixtures (relative mixture effects when negative or positive, respectively) were significantly different from zero. Likewise, relative individual performances were pooled by species across mixtures and were tested against 0 with student t-tests. One-way student t-tests were used for each target species in mixtures to determine if the relative species performances pooled across mixtures differed significantly between the two sites (net site effect on relative individual performances). To determine how site, species richness and species composition affect the relative mixture effects (non-additivity), we used type I analysis of variance. In this model, species richness (from two to four species) and species composition were not considered independent of one another (the sum of these two terms corresponds to the total litter species effect). The factor "species composition" included 28 modalities representing the identity of the 28 mixtures. To analyze relative individual species performance within mixtures, we used a similar model as for the overall response of litter mixtures, with site, mixture identity (i.e. species composition of mixtures) and identity of target species in the mixtures as factors. "Mixture identity" and "target species "were again considered as not independent from each other, or in other words as non-orthogonal variables. Relationships between chemical composition of mixtures or functional diversity indices and mixture mass loss or the relative mixture effects were explored with linear regression analyses. Levels of

significance are indicated as * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$). The R package (version 2.4.0; R Development Core Package 2006) was used for statistical analyses.

Results

Mixture effects on mass loss

Single species mass loss varied among species from 42.1% to 89.5% in the natural forest and from 25.2% to 59.5% in the plantation. Mass loss of mixtures ranged from 46.5% to 73.9% in the natural forest and from 33% to 69% in the plantation. Mass loss of both, single litter species and mixtures was significantly higher in the natural forest (an average of 61.3%) than in the plantation (an average of 45.2%, $F_{1\text{-}44} = 94.3$***, one- way ANOVA).

The relative mixture effect varied strongly among the different litter treatments ranging from clearly negative (up to -26.7%) to strongly positive effects (up to 52.1%). Antagonistic effects (all mixtures showing a mean relative mixture effect lower than 0) were on average significantly lower than zero, in both the natural forest (mean = -8.6 %, $t_{19} = -3.20$**) and in the plantation (mean = -11.8 %, $t_{13} = -4.26$***). Likewise, synergistic effects (all mixtures showing relative mixture effects higher than 0) were on average significantly greater than zero in both the natural forest (mean = 12.7 %, $t_{35} = 6.55$***) and in the plantation (mean = 20.3 %, $t_{41} = 9.31$***). The overall relative mixture effect across all litter treatments resulted in a significant higher effect than 0, both in the plantation (mean = 12.3%, $t_{55} = 4.8$***) and in the natural forest (mean = 5.1%, $t_{55} = 2.4$*). Irrespective of the site, mean relative mixture effects were significantly different among levels of species richness (Table 1). Post-hoc tests (Tukey HSD) revealed that this richness effect was explained by overall lower non-additive effects in 3-species mixtures compared to 2- and 4-species mixtures. However, most of the variation in the relative mixture effect was explained by the species composition of mixtures but this effect differed between the two sites (Table 1).

The separation of litter from individual species included in the mixtures at final harvest allowed us to test for mixture effects on decomposition of individual species within mixtures. The relative individual performance of species within mixtures ranged from -33.6% to 47.5% in the natural forest and from -38% to 96% in the plantation. The identity of mixtures (*i.e.* species composition of mixtures) had a significant influence on relative individual performances of species in mixtures (Table 2). Relative individual performance in mixtures varied considerably among the target species. The identity of target species, explained twice as much of the variance than the identity of mixtures (Table 2). For example, in mixture, *Platonia* litter decomposed significantly slower than expected from single species decomposition at both sites (natural forest: mean = -5.3%, $t_9 = -3.12$**; plantation: mean = -29.3%, $t_9 = -10.55$***), whereas *Caryocar* (natural forest: mean = 27.9%, $t_7 = 2.71$*; plantation: mean = 25.8%, $t_7 = 2.45$*), *Diplotropis* (natural forest: mean = 14%, $t_3 = 3.53$*; plantation: mean

= 20.8%, t_3 = 3.20*), *Sterculia* (natural forest: mean = 14.7%, t_9 = 4.20**; plantation: mean = 15.7%, t_9 = 2.48*), or *Symphonia* (natural forest: mean = 16.7%, t_3 = 7.10**; plantation: mean = 31.6%, t_3 = 10.00**) litter decomposed significantly faster than expected at both sites. However, target species identity interacted significantly with site, showing that relative individual performance in mixtures of certain species differed between sites (Table 2).

Table 1: Results of ANOVA to test for the effects of site, species richness, and species composition on relative mixture effects in litter mixtures. Species richness is the number of species from which leaf litter was mixed and species composition is the combination of species whose leaf litter was in the mixture. These two factors were considered not independent in the analysis.

Source	Df	Sum squares	%Sum squares	Mean squares	*F*-value	*P*-value
Site	1	1429.50	4.07	1429.50	9.82	0.003
Species richness (R)	2	2036.72	5.80	1018.36	7.00	0.002
Species composition (C)	25	10307.68	29.37	412.31	2.83	<0.001
Site x R	2	404.15	1.15	202.07	1.39	0.258
Site x C	25	12770.74	36.39	510.83	3.51	<0.001
Residuals	56	8149.66	23.22	145.53		

Table 2: Results of ANOVA to test for the effects of site, target species and mixture identity on the relative individual performance of target species within mixtures. Target species corresponds to the identity of a given individual species within all mixtures containing this particular species, and mixture identity corresponds to the species composition of mixtures. These two factors were considered not independent in the analysis.

Source	Df	Sum squares	% Sum squares	Mean squares	F-value	*P*-value
Site	1	4404.58	2.03	4404.58	9.05	0.003
Target species (T)	15	49399.99	22.80	3293.33	6.76	<0.001
Mixtures identity (M)	26	25206.16	11.63	969.47	1.99	0.005
Site x T	15	32309.14	14.91	2153.94	4.42	<0.001
Site x M	26	17739.65	8.19	682.29	1.40	0.104
Residuals	180	87642.50	40.44	486.90		

Chemical composition and diversity as drivers of mixture effects?

In order to better understand how species identity controls both observed mass loss and mixture effects, we characterized the chemical composition of mixtures using the eight litter traits measured for the 16 studied species. Observed mass loss across the whole data set (both single species and mixture mass loss) was negatively correlated with initial concentrations in condensed tannins at both sites (natural forest: $r^2 = 0.23^{***}$; plantation: $r^2 = 0.12^{*}$) and in lignin (natural forest: $r^2 = 0.12^{*}$; plantation: $r^2 = 0.19^{**}$). In addition, observed mass loss was positively correlated with initial concentration in hemicellulose (natural forest: $r^2 = 0.18^{**}$, plantation: $r^2 = 0.20^{**}$). None of the other measured litter traits correlated with observed mass loss at either site. We did not find any consistent relation between mean chemical composition of mixtures and relative mixture effects or relative individual performances of any of the species within mixtures. The strong effect of identity of target species in mixtures showed no clear patterns when compared to the litter type specific traits.

We calculated three common diversity indices to test the hypothesis that chemical diversity of litter mixtures explains some of the large variation of the observed mixture mass loss and of the relative mixture effects. The Shannon index was very similar among litter mixtures with only little variation (CV = 0.04, data not shown). Consequently, the Shannon index separates only little along the index axis and could not be used to test our hypothesis. None of the two remaining diversity indices based on all litter traits correlated with the mixture mass loss or with the relative mixture effects at either site (Fig. 1). In an attempt to include only the functionally most relevant traits, the diversity indices were additionally calculated with the subset of litter traits that significantly correlated with observed mass loss at both sites (i.e condensed tannins, lignin and hemicellulose). However, diversity indices calculated using only the subset of litter traits also failed to show any significant relationships between functional diversity and mixture mass loss or relative mixture effects at both sites. Similar to the overall responses of mixtures, the relative individual performance of species within mixtures did not correlate with any of the diversity indices calculated for the whole mixture (data not shown).

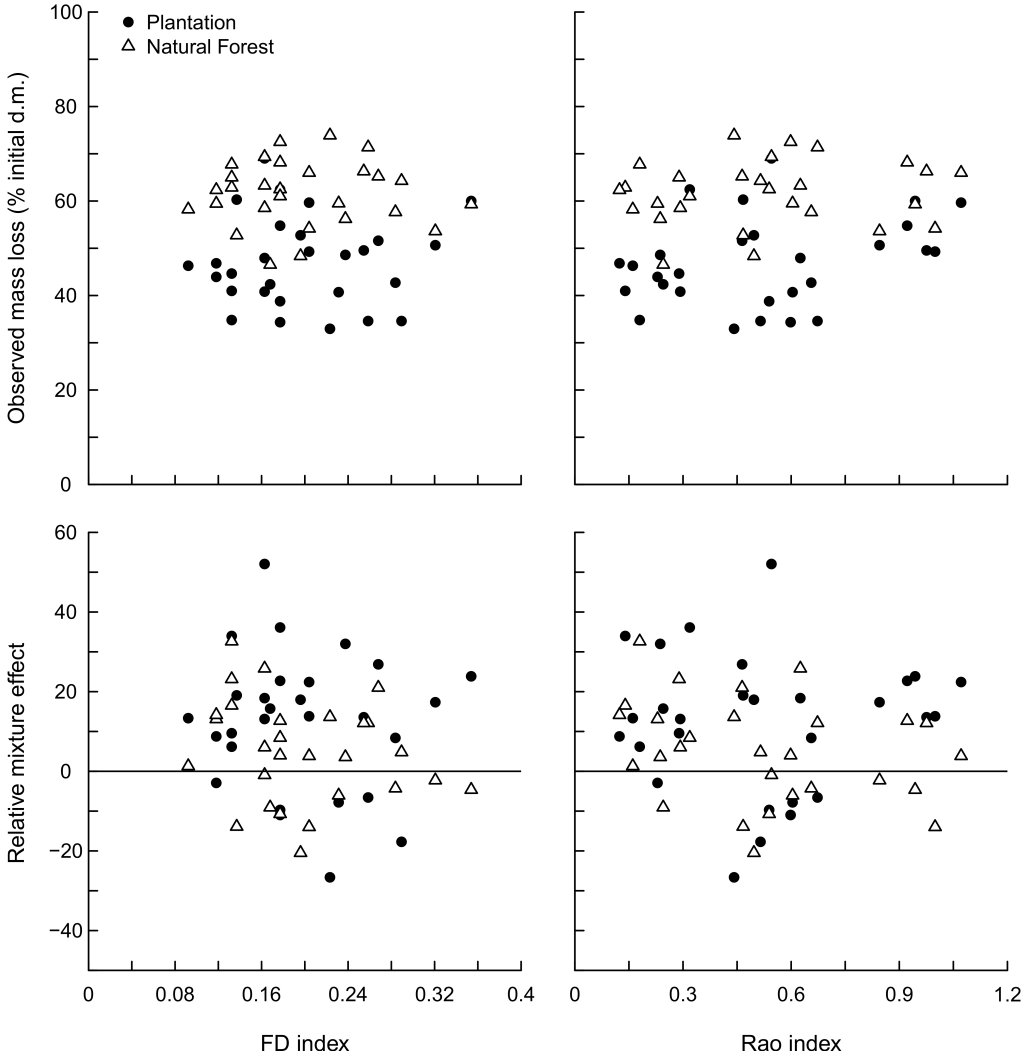

Figure 1: Observed mass loss and mean relative mixture effect ((observed mass loss – expected mass loss) / expected mass loss x 100) for each of the 28 different litter mixtures as a function of chemical litter diversity. Chemical litter diversity was expressed as the FD index (left panel) and as the Rao index (right panel). Black circles indicate the 28 mixtures exposed at the site of origin in the plantation, and open triangles indicate the same 28 mixtures exposed at the common site in the natural forest.

Effects of long-term presence of tree species

Our experimental design allows to specifically test the impact of long-term presence of tree species on litter mixture effects through continuous litter input and root activity. The mean relative mixture effect across all mixtures was positive at both sites (see above) and significantly higher in the plantation compared to the natural forest (Table 1). Calculating the net site effect (i.e. the mean relative mixture effect in the plantation minus the mean relative mixture effect in the natural forest) showed an overall positive net site effect of 7.2% on average across all mixtures. However, this site effect was not consistent across the different

mixtures as indicated by the significant interaction between site and litter composition (Table 1). 18 litter mixtures showed positive net site effects (i.e. stronger mixture effects in the plantation than in the natural forest) with a maximum of 52% (for *Simarouba* – *Goupia* mixture) (Fig. 2). The remaining 10 litter mixtures showed negative net site effects (resulting both of weaker synergistic effects or higher antagonistic effects in the plantation than in the natural forest) with a maximum of -40% (for *Platonia* – *Caryocar* – *Hymenea* mixture). The relative individual performances of species within mixtures also differed between sites (Table 2), reflecting the fact that positive mixing effects on individual species performance were stronger and more frequent in the plantation than in the natural forest (Fig. 3). The overall net site effect resulted in a 10.3% positive difference in relative individual performances on average across all 16 litter species. This influence of long-term presence of tree species depended on species identity (Fig. 3), as shown by the significant site x target species interaction (Table 3). Six litter species showed a significantly greater positive response to mixing when decomposing in the plantation, i.e. with the direct and long-term influence of the corresponding tree species represented in the litter mixtures (Fig. 3). In contrast, leaf litter from the two species *Platonia* and *Eperua* within mixtures showed a significantly smaller response to mixing when decomposing in the plantation than in the natural forest (Fig. 3). A total of eight litter species showed no significant difference in individual performance within mixtures between the two forest sites (Fig. 3).

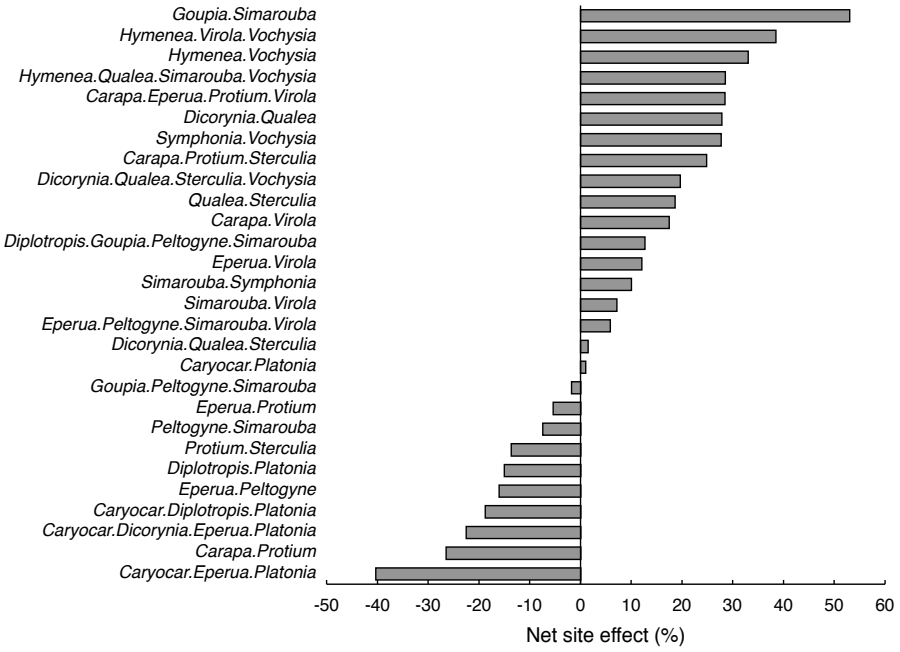

Figure 2: Net site effect for the 28 different litter mixtures (species names of litter composing the respective mixtures are indicated at the left). The net site effect was calculated for each mixture as the mean relative mixture effect in the plantation minus the mean relative mixture effect in the natural forest. A positive net site effect thus indicates a more positive or less negative relative mixture effect in the plantation than in the natural forest, while a negative net site effect indicates a more negative or less positive mixture effect in the plantation than in the natural forest.

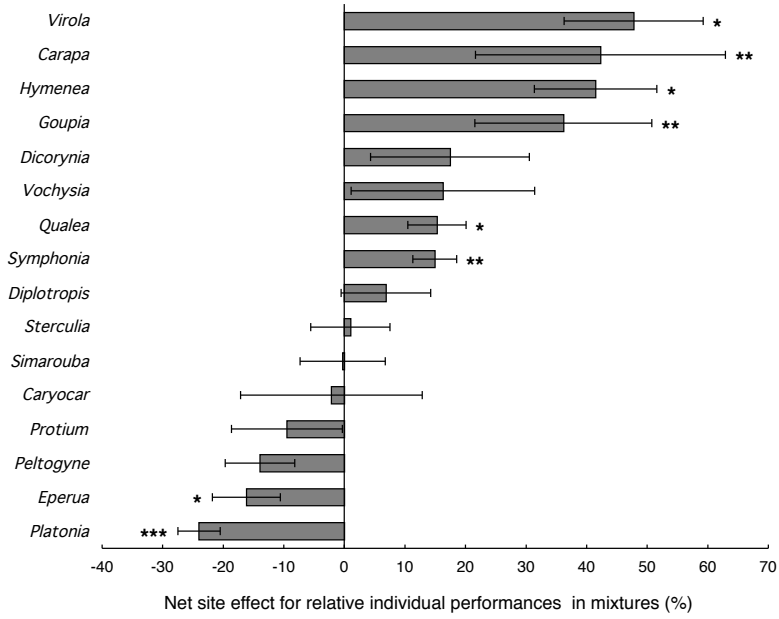

Figure 3: Net site effect for the 16 individual "target" species (species names indicated at the left) within the 28 different litter mixtures (mean ± SE). Similar to Fig. 2, the net site effect was calculated for each mixture as the mean relative individual performance of each "target" species within mixtures in the plantation minus the mean relative individual performance of the same "target" species within the same mixtures in the natural forest. Symbols denote the level of significance of unpaired t-tests to test if relative individual performance differed between sites (* < 0.05, **<0.001, *<0.0001).**

Discussion

Effects of litter diversity on decomposition

Apart of a negligible and non-linear effect of species richness in litter mixtures exposed in the plantation, the non-additive effects were mostly driven by species composition, i.e. by the identity of component species. This result contributes to the growing evidence across different ecosystems that the number of species included in litter mixtures is quite unimportant compared to their composition for the prediction of litter mixture decomposition (Wardle *et al.*, 1997, Ball *et al.*, 2008, Jonsson & Wardle, 2008, Hättenschwiler & Bracht Jørgensen, 2010). Non-additive effects were frequent in our study with mean positive (synergistic) mixture effects between 12.7% (natural forest) and 20.3% (plantation) and mean negative (antagonistic) mixture effects between -8.6% (natural forest) and -11.8% (plantation). Such differences compare well with the mean non-additive effects observed across multiple studies from mainly temperate ecosystems (reviewed by Gartner & Cardon, 2004) and can have important consequences for biogeochemical cycling over the longer term. As an example, a modelling study by Finzi and Canham (1998) showed that even small interactions, applied over larger spatial and temporal scales, can have significant consequences for N cycling in a temperate forest.

Conceptual and empirical attempts of understanding the underlying mechanisms of litter mixture effects have focussed on litter chemistry traits (e.g. Hättenschwiler *et al.*, 2005; Epps *et al.*, 2007) as a major driver of decomposition (Swift *et al.*, 1979; Cornwell *et al.*, 2008). In our study, observed mass loss across all litter treatments correlated best with initial mean condensed tannin and lignin concentrations (negatively) and with mean hemicellulose concentrations (positively), but with none of the nutrient related litter quality traits. Carbon quality rather than nutrient control has previously been suggested for our study system (Hättenschwiler & Bracht Jørgensen, 2010), and the particularly strong effect of condensed tannins is in line with a recent study of mono-specific litter decomposition in the same rainforest (Coq *et al.*, 2010). However, the relative litter mixture effects on decomposition observed in our study were not related to mean concentrations of condensed tannins, lignin, and hemicellulose or to any of the other measured litter quality traits. Similarly, the relative performance of individual litter species within mixtures did also not correlate with any of the average litter quality traits of the mixtures. The lack of correlation between mixture effects and average traits of litter mixtures suggests that mean litter mixture chemistry is not relevant for the understanding of non-additive effects of mixed litter species decomposition. This is not too surprising, because mechanistically, mixture effects are expected to occur when chemically distinct litter types provide complementary resources to decomposers, or

allow nutrient transfer among litter types (Hättenschwiler *et al.*, 2005; Epps *et al.*, 2007), which is not reflected in mean chemical litter traits.

Accordingly, our first hypothesis stated that litter mixture effects increase with increasing chemical heterogeneity or functional (litter chemistry) diversity of mixtures. In contrast to this hypothesis, neither chemical richness (FD index) nor chemical divergence (Rao index) correlated with litter mixture effects or even with the overall observed mass loss of mixtures (Fig. 1). Our study differs from most previous litter mixture experiments in that we separated litter from all individual species within mixtures at the end of the experiment. This allowed us to identify strong species-specific responses in mixtures. An important result was that the relative individual performance of the various litter types depended more strongly on the identity of target species than on the identity of neighbour species contained in the mixture. Some species showed quite consistent responses independently of the site of incubation and of the identity of litter from other species in the mixtures. For example, litter from *Platonia* generally decomposed slower than predicted, and litter from *Diplotropis*, *Caryocar*, *Sterculia* and *Symphonia* decomposed faster than predicted, regardless of mixture species composition. Moreover, the relative individual performance of the different litter types did also not correlate with chemical diversity of mixtures, suggesting that characteristics of individual litter types rather than those of litter mixtures determine their decomposition within mixtures. Collectively, these results suggest that the observed mixture effects depend on the presence of "responsive" litter types that are not or only little influenced by the identity and characteristics of the other litter types present in the mixture. This would explain why there was no apparent effect of functional litter diversity on mixture decomposition in our study. More generally, such effects might be responsible for a large part of the idiosyncratic litter diversity effects on decomposition reported in the literature (Wardle *et al.*, 1997; Hättenschwiler *et al.*, 2005). The "responsiveness" of some litter types within mixtures may be explained with dilution effects. For example, decomposition of recalcitrant litter species rich in inhibiting compounds may be accelerated in mixtures because the inhibiting compounds are less concentrated allowing a more abundant or efficient decomposer community per unit mixed litter mass. *Diplotropis*, *Caryocar*, and *Sterculia* litter that decomposed faster than predicted in any of the mixtures actually are relatively recalcitrant and would illustrate this interpretation. Other litter types that are preferentially consumed by detritivores such as *Platonia* (Coq *et al.*, 2010) might be more hidden in mixtures and would therefore tend to decompose more slowly than in mono-specific litter patches in line with our findings.

Few other studies investigated explicitly the role of functional diversity on litter mixture decomposition. Two studies specifically testing for this, did not find any correlation between trait diversity and non-additive effects (Hoorens *et al.*, 2003; Schindler & Gessner,

2009). However, Hoorens *et al.* (2003) defined functional diversity as the absolute difference in single litter traits between two litter types, and Schindler and Gessner (2009) assessed functional diversity by simple comparisons between heterogeneous (i.e. including species with different decomposition rates) vs. homogeneous mixtures (i.e. mixtures of litter types with similar decomposition rates). Defining functional diversity on single traits or distinguishing functional groups based on *a priori* information of the response variable are not ideal to test for the effect of functional diversity on mixed litter decomposition. In another study, soil respiration, net nitrogen mineralization and non-additive net nitrogen mineralization in litter mixtures of four alpine plant species were well predicted with a measure of functional diversity based on Shannon's index calculated from 9 chemical mostly carbon related traits (Meier & Bowman, 2008, 2010).

Overall, we found little evidence for the predictability of relative mixture effects on either individual litter species responses or whole mixture responses based on the functional traits measured. Collectively, our results suggest that at our study site the presence of particular species in mixtures is more important than functional diversity of the mixture for non-additive mixture effects. Hence, litter mixtures do not respond as an entity, but component species might be affected quite independently of the identity of associated species.

Site effect

Our results clearly demonstrated that the location of exposure of decomposing litter influenced the overall rates of decomposition. Regardless of litter treatment, litter decomposition in the natural forest proceeded faster than in the neighbouring plantation. Both sites share the same macroclimate and soil type with largely the same average soil texture and elemental composition. Higher rates of decomposition in the natural forest may be related to more favourable microclimatic conditions or to differences in the abundance and composition of soil fauna communities.

While the additive effects of litter composition and the associated average litter quality traits as the main drivers of observed decomposition were essentially the same in the natural forest and the plantation, the non-additive mixture effects differed considerably between the two sites. It has been argued that the relation between biodiversity and ecosystem processes is context dependent (Cardinale *et al.*, 2000) and multi-site experiments have shown that non-additive effects in litter mixtures can change depending on habitat conditions (Gartner & Cardon, 2006; Madritch & Cardinale, 2007; Jonsson & Wardle, 2008). We initially hypothesized that relative mixture effects should be stronger and more frequent in the plantation due to modifications of the soil environment by the long-term presence of tree species. Such long-term modifications could result from rooting patterns, root processes

related to nutrient foraging and rhizodeposition, and from long-term input of a particular litter type (Hobbie, 1992; Binkley & Giardina, 1998) and could alter the physical environment (pH, nutrient availability) or soil communities (Eviner & Chapin, 2003b). Our results generally support the initial hypothesis. Both, the antagonistic and synergistic non-additive effects were stronger in the plantation than in the natural forest. Moreover, the majority of the 28 litter mixtures showed positive net site effects, i.e. more positive mixture effects in the plantation than in the natural forest, and most litter species showed a more positive relative individual performance in the plantation than in the natural forest (Fig. 3). These results suggest that the long-term presence of canopy trees intensifies mixture effects on decomposition of their own litters. Remarkably, such intensified mixture effects in the plantation led to a higher observed mass loss of 69% in the *Simarouba-Goupia* mixture than in the most rapidly decomposing mono-specific litter treatment (*Hymenea* with 59.5% of mass loss). A performance of a litter mixture higher than the best performing single species litter, known as transgressive overyielding in the biodiversity-ecosystem functioning literature, has, to our knowledge never been reported before. Long-term input of a particular litter type might lead to local adaptation of decomposers that preferentially decompose the litter from that species, also known as the "home field advantage" (Hunt *et al.,* 1988; Vivanco & Austin, 2008; Ayres *et al.,* 2009). We show here that such home field advantage may not only increase observed mass loss of locally produced litter, but that it can also intensify non-additive mixture effects. This suggests that a specialized decomposer community increases the efficiency in complementary resource use of a recurrent heterogeneous resource input from the canopy. Unfortunately, the separation of individual litter types within mixtures upon final harvest did not allow an assessment of the abundance and structure of decomposer communities that might have allowed a better interpretation of the intensified mixture effects in the plantation. Other studies reported an instantaneous increase in abundance and diversity of microbial communities (Chapman & Newman, 2010) and shifts in communities of nematodes and macrofauna (Wardle *et al.,* 2006) in response to artificially created litter mixtures. However, these decomposer community changes did not explain non-additive effects on mixture decomposition in these former studies. In summary, our results support the idea that complementary effects on mixed litter decomposition may emerge and intensify through long-term interactions between aboveground and belowground biota.

Conclusions

Using a large number of litter mixtures from a broad range of different Amazonian rainforest tree species, our study showed that non-additive litter mixture effects on decomposition are common in this highly species rich ecosystem. Positive relative mixture effects were more frequent than negative effects, and they were more pronounced with a long-term presence of the particular tree species contributing to the mixed litter patches. This

suggests that decomposer communities adapted towards complementary use of resources of a regular and long-term availability. Despite the assessment of a large number of litter traits and the use of different approaches to characterize functional diversity of litter mixtures our data provided no evidence that chemical diversity, at least on the basis of the traits measured here, helps to understand why mixed litter decomposition deviates from predictions.

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Appendix Leaf litter chemical composition and observed mass loss of the 16 tropical tree species (species family names are mentioned in bracket) and the 28 litter mixtures (the chemical composition of mixtures was calculated as the average of the relative contribution of each species-specific chemical trait). All data refer to % dry matter (Mean). N = nitrogen, P = phosphorus, Cell = cellulose, HemiC = hemicellulose, Sphen = soluble phenolics, Tphen = total phenolics, CT = condensed tannins. Chemical analyses are described in Coq et al. (2010)

Species composition	Species richness	N	P	Cell	HemiC	Lignin	Sphen	Tphen	CT	Mass loss (%)	
										natural forest	plantation
Carapa procera (Meliaceae)	1	0.94	0.019	22.7	7.5	37.5	2.8	8	2.8	48	28.3
Caryocar glabrum (Caryocaraceae)	1	0.79	0.022	16.8	11.1	34.3	1.5	8	0.9	51.5	33.9
Dicorynia guianensis (Caesalpiniaceae)	1	1.2	0.022	22.5	6.8	44.2	1	4.1	1.5	50.3	33.4
Diplotropis purpurea (Caesalpiniaceae)	1	1.29	0.021	18.7	9.6	33.7	3.3	9.8	3.5	50.9	25.2
Eperua falcata (Caesalpiniaceae)	1	1.1	0.03	20.6	9.1	33.1	1.5	8.8	1.3	55.1	48.9
Goupia glabra (Goupiaceae)	1	1.21	0.033	18.8	16.2	28.4	1.1	2.8	0.2	89.5	51.5
Hymenea courbaril (Caesalpiniaceae)	1	1.22	0.056	22.3	10.3	36.3	1	4.2	1.4	80.5	59.5
Peltogyne venosa (Caesalpiniaceae)	1	0.99	0.018	20.5	11	32.5	0.8	3.1	0.8	50.1	41.7
Platonia insignis (Clusiaceae)	1	1.42	0.018	22.5	23.5	24.7	1	12.5	0.1	88.5	52
Protium sagotianum (Burseraceae)	1	0.94	0.029	21.2	8.4	35.4	1.4	6.8	1	54.2	37.2
Qualea rosea (Vochysiaceae)	1	0.75	0.018	19.4	27.8	11.9	1.4	2.7	0.5	75.7	53.2
Simarouba amara (Simaroubaceae)	1	1.11	0.032	20	11.7	22.8	4.4	11	2.3	50.5	39.3
Sterculia pruriens (Sterculiaceae)	1	1.07	0.028	22.1	9.2	42.9	2.5	5.9	3.1	51.4	44.3
Symphonia sp. (Clusiaceae)	1	1.02	0.016	26.3	22	25.2	0.6	3.8	0.3	70.5	50
Virola surinamensis (Meliaceae)	1	0.82	0.033	17.3	12.1	35.8	2.6	6.6	2.5	59.9	32.9
Vochysia tomentosa (Sterculiaceae)	1	0.87	0.028	19.7	20.1	25.6	0.6	4.4	1.4	42.1	41.8
Carapa / Virola	2	0.88	0.026	20	9.8	36.6	2.7	7.3	2.7	62.9	41
Eperua / Peltogyne	2	1.04	0.024	20.6	10.1	32.8	1.1	6	1	59.5	43.9
Eperua / Virola	2	0.96	0.032	19	10.6	34.4	2	7.7	1.9	58.2	46.3
Caryocar / Platonia	2	1.11	0.02	19.6	17.3	29.5	1.2	10.3	0.5	62.5	38.8
Diplotropis / Platonia	2	1.36	0.019	20.6	16.5	29.2	2.1	11.2	1.8	72.5	34.4
Carapa / Protium	2	0.94	0.024	21.9	7.9	36.4	2.1	7.4	1.9	67.8	34.8
Eperua / Protium	2	1.02	0.03	20.9	8.7	34.2	1.4	7.8	1.1	62.4	46.8

Dicorynia / Qualea	2	0.98	0.02	20.9	17.3	28.1	1.2	3.4	1	54.2	49.3
Qualea / Sterculia	2	0.91	0.023	20.8	18.5	27.4	2	4.3	1.8	66	59.7
Goupia / Simarouba	2	1.16	0.033	19.4	14	25.6	2.7	6.9	1.2	69.4	69
Peltogyne / Simarouba	2	1.05	0.025	20.3	11.4	27.7	2.6	7.1	1.5	63.3	47.9
Protium / Sterculia	2	1.01	0.029	21.7	8.8	39.2	2	6.4	2	65	44.7
Simarouba / Symphonia	2	1.06	0.024	23.1	16.9	24	2.5	7.4	1.3	68.2	54.8
Symphonia / Vochysia	2	0.95	0.022	23	21.1	25.4	0.6	4.1	0.9	61	62.4
Simarouba / Virola	2	0.96	0.032	18.7	11.9	29.3	3.5	8.8	2.4	58.5	40.8
Hymenea / Vochysia	2	1.04	0.042	21	15.2	31	0.8	4.3	1.4	52.8	60.3
Hymenea / Virola / Vochysia	3	0.97	0.039	19.8	14.2	32.6	1.4	5.1	1.8	48.4	52.8
Goupia / Peltogyne / Simarouba	3	1.1	0.028	19.8	13	27.9	2.1	5.7	1.1	59.5	40.7
Caryocar / Diplotropis / Platonia	3	1.17	0.02	19.3	14.7	30.9	1.9	10.1	1.5	71.4	34.6
Caryocar / Eperua / Platonia	3	1.1	0.024	20	14.6	30.7	1.3	9.8	0.8	73.9	33
Dicorynia / Qualea / Sterculia	3	1.01	0.023	21.3	14.6	33	1.6	4.2	1.7	66.3	49.6
Carapa / Protium / Sterculia	3	0.99	0.026	22	8.3	38.6	2.3	6.9	2.3	46.5	42.4
Carapa / Eperua / Protium / Virola	4	0.95	0.028	20.5	9.3	35.4	2.1	7.5	1.9	56.2	48.6
Caryocar / Dicorynia / Eperua / Platonia	4	1.13	0.023	20.6	12.6	34.1	1.2	8.4	1	64.3	34.6
Hymenea / Qualea / Simarouba / Vochysia	4	0.99	0.034	20.4	17.5	24.2	1.8	5.6	1.4	59.3	60
Diplotropis / Goupia / Peltogyne / Simarouba	4	1.15	0.026	19.5	12.1	29.4	2.4	6.7	1.7	57.7	42.7
Dicorynia / Qualea / Sterculia / Vochysia	4	0.97	0.024	20.9	16	31.2	1.4	4.3	1.6	53.6	50.7
Eperua / Peltogyne / Simarouba / Virola	4	1	0.028	19.6	11	31	2.3	7.4	1.7	65.2	51.6

Synthèse

La diversité fonctionnelle des producteurs primaires, *via* la qualité de leurs litières, influence la décomposition et le recyclage des nutriments en forêt Amazonienne

La diversité spécifique élevée des arbres de forêt amazonienne (environ 150 espèces par hectare sur notre site d'étude) se traduit par une forte diversité fonctionnelle, avec notamment une large gamme de variation des traits foliaires parmi les espèces co-existantes (Townsend *et al.*, 2007; Hättenschwiler *et al.*, 2008; Baraloto *et al.*, 2010). Cette diversité se traduit localement par des apports de litière très hétérogènes, avec en particulier de fortes variation de la stœchiométrie C:N:P et de la qualité des formes de C dans les assemblages de litières (en fonction du nombre et du type de litières présentes) (Hättenschwiler *et al.*, 2008; Fanin *et al.*, 2011). Les différentes études que j'ai mené au cours de cette thèse ont permis de mettre en évidence que cette forte hétérogénéité de la qualité des litières, non seulement imposait d'importantes contraintes nutritives sur les organismes décomposeurs, mais favorisait aussi des effets synergiques dans les mélanges de litières. Ainsi, la diversité végétale impacte la décomposition et le recyclage des nutriments à la fois à travers des effets de composition (identité des espèces présentes), et à travers des effets d'interactions (combinaisons particulières d'espèces).

I. Les effets des variations de la qualité des litières sur la décomposition et le recyclage des nutriments :

Des études antérieures sur notre site d'étude ont montré qu'il n'y avait pas de corrélation entre les taux de décomposition et la concentration en nutriments des litières (ni même avec les rapports communément utilisés du type C:nutriments ou lignine : nutriments) (Coq *et al.*, 2010). En revanche, les taux de décomposition apparaissaient fortement corrélés à des traits reliés à la qualité du C, tels que des composés inhibiteurs (tanins condensés) ou bien des composés carbonés riches en énergie et facilement accessibles (amidon, sucres, phénols de faible poids moléculaire). Sur la base de ces études, Hättenschwiler et collaborateurs (2011) (Cf *Annexe A*) suggèrent que les décomposeurs dans cette forêt seraient primairement limités par l'énergie (*via* la qualité du C) plutôt que par les nutriments. L'un des objectifs clés de ma thèse était de déterminer de façon expérimentale comment les variations interspécifiques de la qualité des litières modulaient les limitations énergétiques et nutritionnelles des organismes décomposeurs.

A. Synthèse des résultats acquis

Pour tester l'hypothèse selon laquelle le fonctionnement des organismes décomposeurs est d'abord limité par l'accès à l'énergie (*via* la qualité du carbone), puis par l'accès aux nutriments, des expérimentations basées sur des ajouts factoriels de cellulose, d'azote et de phosphore à des litières de différentes espèces d'arbres (seules ou en mélanges) ont été mises en place en laboratoire et en forêt naturelle. Avec ces dispositifs expérimentaux, nous voulions tester si :

(i) l'activité des micro-organismes et la décomposition seraient stimulées par l'ajout de cellulose (une forme carbonée relativement riche en énergie et facilement accessible pour une grande majorité d'organismes décomposeurs) *via* un « priming effect» (le « priming effect » correspondant à une stimulation de la dégradation de la matière organique récalcitrante, suite à l'addition de C labile riche en énergie).

(ii) une fois la contrainte énergétique levée, les ajouts de nutriments stimuleraient la décomposition.

(iii) la levée simultanée des contraintes énergétiques et nutritionnelles aurait des effets synergiques positifs sur le processus de décomposition.

Contrairement à notre première hypothèse, la décomposition (perte en masse des litières), en forêt et en laboratoire, n'a généralement pas été stimulée par les ajouts de cellulose, et a même diminué quand la cellulose était ajoutée seule (sans les nutriments) (*chapitre 1, chapitre 2*). Des mesures plus précises du fonctionnement des communautés microbiennes en laboratoire ont montré que les ajouts de cellulose stimulaient la respiration totale des communautés microbiennes dans les microcosmes (*chapitre 1*). **Les décomposeurs ont donc préférentiellement utilisé cette source de carbone, plutôt que la matière organique plus complexe des litières.** En d'autres termes, nous n'avons pas observé de « priming effect » (*chapitre 1, chapitre 2*).

L'un des résultats important de nos deux expérimentations, tant en conditions contrôlées qu'*in situ*, repose sur une apparente co-limitation en N et P de la décomposition. En effet, alors que des ajouts de ces nutriments séparément n'avaient que peu d'effets sur la décomposition, leur addition conjointe stimulait fortement à la fois le fonctionnement des communautés microbiennes (*chapitre 1*) et la décomposition (*chapitres 1 et 2*). De plus, ces effets étaient significativement plus importants en présence de la faune saprophage (*chapitre 2*). **Finalement, nous avons montré que l'étendue de cette co-limitation en nutriments est largement contrôlée par la disponibilité en P des feuilles, mais également reliée à leurs stœchiométries N:P et C:P** (*chapitres 1 et 2*).

Ces résultats mettent en évidence l'importance de manipuler les différentes ressources de manière factorielle, afin de comprendre les effets de la qualité nutritionnelle des litières sur les activités des décomposeurs. Quelques études avaient précédemment effectué des manipulations factorielles de C, N et P (Scheu & Schaefer, 1998; Teklay *et al.*, 2006; Reed *et al.*, 2011), mais ces expérimentations considéraient uniquement les effets des ajouts de ressources sur la respiration ou la biomasse des communautés microbiennes ou détritivores (Scheu & Schaefer, 1998), et non les effets sur la décomposition de la matière

organique. La limitation en nutriments de la décomposition a été largement considérée dans les biomes tempérés, à travers des expériences de fertilisation azotée (voir Knorr *et al.,* 2005 pour une synthèse), mais il existe peu d'études portant sur la limitation en nutriment P et/ou N en forêt tropicale (Hobbie & Vitousek, 2000; Mcgroddy *et al.,* 2004b; Kaspari *et al.,* 2008). Notre approche, en combinant des ajouts factoriels de C, N, P à une large gamme de stœchiométrie N : P des litières, nous a permis de montrer que la décomposition des litières en forêt de Paracou était limitée conjointement par N et P, et que l'amplitude de cette co-limitation était fortement reliée à la disponibilité en P de la litière.

B. Quels mécanismes pour expliquer l'effet des ajouts de ressources C, N, P sur la décomposition ?

L'identification, via des expériences de fertilisation, des limitations énergétiques et nutritionnelles des organismes décomposeurs est importante pour prédire de façon mécaniste comment la qualité de la ressource impacte la décomposition et le recyclage des éléments C, N et P. Cependant, la mise en évidence de ces limitations (en particulier la limitation énergétique), et la compréhension des mécanismes sous-jacents à la co-limitation NP, peuvent s'avérer complexes.

1- Une famine en énergie ?

Si les approches corrélatives indiquent une forte contrainte de la qualité du C sur la décomposition, la mise en évidence expérimentale de cette contrainte énergétique (à travers les ajouts de composés carbonés facilement utilisables par les décomposeurs) est complexe. Les mécanismes du « priming effect », et les facteurs qui peuvent l'influencer, sont encore relativement mal connus (Blagodatsky *et al.*, 2010; Kuzyakov, 2010). Il a été proposé que le « priming effect » résulte de l'intensité de compétition entre des micro-organismes à stratégie-r (à fort taux de croissance, utilisant des formes de C riche en énergie), et des micro-organismes à stratégie-K utilisant les formes récalcitrantes du C (Fontaine *et al.*, 2003). Selon ce modèle, une plus forte utilisation de la MO récalcitrante suite à l'ajout de C labile est possible seulement si les micro-organismes à stratégie K deviennent plus compétitifs et

utilisent une partie substantielle du C labile ajouté. Cependant le « priming effect » pourrait aussi résulter d'une stimulation des activités métaboliques des micro-organismes, favorisant la production d'enzymes énergétiquement plus coûteuses pour dégrader le C récalcitrant (Kuzyakov *et al.*, 2000). Dans notre expérimentation en laboratoire (*chapitre 1*) nous avons mis en évidence une augmentation des activités enzymatiques impliquées dans la dégradation des formes complexes de C (peroxidase, laccase) relativement à celles impliquées dans l'utilisation des formes plus simples du C (cellulase, hemicellulase, β-glucosidase). Ces activités étaient mesurées à la fin de l'expérimentation, et suggèrent l'existence d'un effet priming à plus long terme. L'analyse de la composition des communautés microbiennes en réponse à ces ajouts de cellulose sur le dispositif expérimental *in situ* permettrait de comprendre s'il s'agit simplement d'une simple utilisation préférentielle de cette source de C, ou d'un changement de la composition des communautés.

Enfin, afin de mieux comprendre le rôle de la qualité du C, il serait intéressant de tester les effets de différentes formes biochimiques du C (phénols, composés organiques dissous, tanins condensés …) sur la décomposition et les activités des détritivores et des microorganismes.

2- Mécanismes potentiels de la co-limitation NP :

a) les différents groupes de décomposeurs ont des besoins stœchiométriques différents

La théorie de l'écologie stœchiométrique est largement basée sur la loi de Liebig (Sterner & Elser, 2002). Cette théorie prédit qu'un organisme sera primairement limité par l'élément en plus faible disponibilité relativement aux autres, en fonction de ses exigences stœchiométriques. Si la loi de Liebig est assez robuste quand elle s'applique à l'échelle d'un organisme, elle est plus difficile à appliquer à l'échelle d'une communauté d'espèces, qui peuvent avoir des besoins stœchiométriques différents (Danger *et al.*, 2008).

La décomposition est conduite par une grande diversité d'organismes décomposeurs qui ont des besoins nutritifs différents en fonction de leur composition élémentaire. La stœchiométrie N:P varie en fonction des différents taxons de détritivores, et par exemple, les bactéries ont des besoins en nutriments plus élevés que celui des champignons (Smith, 2002;

Martinson *et al.*, 2008). Une forte variation dans les besoins des différentes espèces pourrait ainsi contribuer à un mécanisme de co-limitation du processus de décomposition.

Il n'existe actuellement, à notre connaissance, aucune étude ayant évalué les limitations du processus de décomposition par des ajouts combinés de ressources externes (C, N, P) en lien avec la stœchiométrie des organismes et la composition des communautés de décomposeurs. **La caractérisation de la stœchiométrie de la biomasse microbienne et des détritivores est actuellement en cours sur le dispositif de fertilisation en forêt naturelle. Cette caractérisation, en lien avec les ajouts de ressources, constituera une étape importante pour comprendre les limitations nutritives des organismes.**

b) les éléments N et P sont stabilisés différemment dans les substrats organiques

Les éléments N et P ne sont pas stabilisés de la même façon dans la matière organique (Mcgill & Cole, 1981). L'azote est directement imbriqué au squelette carboné des composés organiques, tandis que le phosphore est associé au carbone à travers des liens esters. L'azote est ainsi distribué dans plusieurs classes de polymères, et son acquisition dépend d'une vaste gamme d'enzymes extracellulaires (Caldwell, 2005). Le phosphore est lui plus directement obtenu grâce à l'activité des phosphatases, qui permettent de rompre les liaisons ester. La stratégie d'acquisition de l'N est donc plus complexe que celle du P, et peut être fortement liée aux stratégies d'utilisation du C (Manzoni *et al.*, 2008). Ainsi, l'activité phosphatase reflète souvent directement la disponibilité en phosphore et donc les besoins en P des micro-organismes (Olander & Vitousek, 2000). A contrario, les relations entre la disponibilité en N et les activités des enzymes reliées à son acquisition (comme les chitobiases par exemple) sont moins évidentes (Sinsabaugh *et al.*, 2008). Ainsi, dans le *chapitre 1*, nous avons montré que la phosphatase était fortement diminuée en présence de P, tandis que la chitobiase répondait peu aux ajouts d'N.

A la lumière de ces différences de couplage entre les éléments N et P avec les formes carbonées, nous avons proposé une explication de la relation entre l'apparente co-limitation en NP de la décomposition et la stœchiométrie N:P des litières (*chapitre 1*). L'augmentation des effets des ajouts conjoints de N et P avec la diminution du contenu en P des feuilles

(relativement à celui de N), suggère que le contenu en P des feuilles est plus profondément limitant pour la décomposition. En effet, les litières contiennent comparativement moins de P que de N. Cependant, la minéralisation de l'N nécessite une dégradation de molécules carbonées complexes, alors que le P des litières peut être plus directement utilisé. Autrement dit, le P serait initialement plus accessible que l'N, et la décomposition serait initialement limitée en N. Ainsi, sans ajout d'azote minéral, le P ajouté ne pourrait être utilisé. De façon similaire, l'ajout de N seul ne suffirait pas à lever la contrainte nutritionnelle car la faible quantité de P présente serait rapidement limitante. Enfin, le P, en plus faible quantité dans les litières, apparait comme ultimement limitant. Dans une expérimentation complémentaire à celle réalisée en laboratoire (*chapitre 1*), Jean Marchal, (2010, rapport de master 2) a étudié les dynamiques temporelles de décomposition des litières de 3 espèces d'arbres (*Platonia*, *Hymenea*, *Vochysia*) en fonction des ajouts de N et P. Dans cette étude, il apparaissait que, au cours des deux premiers mois d'incubation, les ajouts de N seul stimulaient la perte en masse de litière de *Platonia*, puis cet effet positif de l'N disparaissait, tandis que l'ajout de P seul stimulait la décomposition dans une deuxième phase (Fig 9). Les ajouts simultanés de NP étaient cependant toujours supérieurs aux effets des nutriments seuls. Cette dynamique observée en conditions contrôlées renforce notre interprétation, et pour mieux comprendre comment l'ajout d'une des deux ressources influence la demande pour l'autre ressource, il serait intéressant d'effectuer des ajouts combinés NP avec une large gamme de ratio.

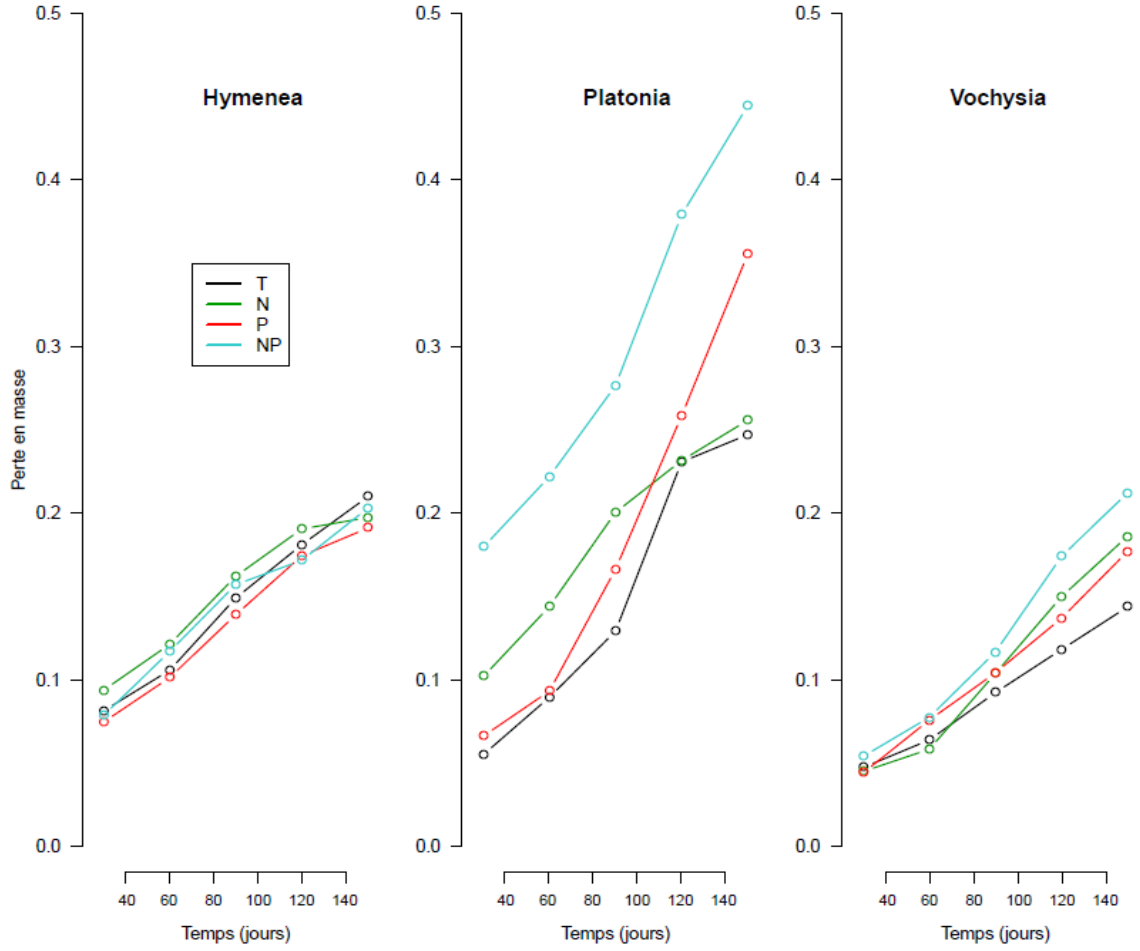

Figure 9: Evolution de la constante de décomposition (k) des litières des 3 espèces *Hymenea Courbaril*, *Platonia insignis*, *Vochysia tomentosa* en fonction de l'ajout des ressources N et P (T : traitement témoin sans fertilisation en noir, + N en vert ; +P en rouge et + NP en bleu) au cours de 5 mois d'incubations en microcosmes (d'après Marchal, 2010).

c) le rôle de la faune

Nous avons mis en évidence que l'effet de l'ajout de N et P sur la décomposition était plus élevé en présence faune (*chapitre 2*). En parallèle, des données préliminaires sur le dispositif ont mis en évidence que l'abondance des détritivores était stimulée par ces ajouts (Johanne Nahmani, *comm.pers*). Cette stimulation de la biomasse peut résulter :

- d'un effet indirect à travers la stimulation de la biomasse microbienne. En effet, les micro-organismes de la litière constituent une source importante du régime

alimentaire de certains détritivores (Kurihara & Kikkawa, 1986). Ainsi, l'augmentation de la biomasse microbienne, par ajout de N et P, stimulerait à son tour l'abondance des détritivores.

- et/ou d'un effet direct de l'ajout des nutriments.

Ce dernier point apparaît important à approfondir, très peu d'études existant sur la limitation en nutriment des détritivores. En effet, les détritivores sont souvent supposés limités par une quantité de ressource, et non par la composition chimique de la ressource (Scheu & Schaefer, 1998). **Dans notre système d'étude, la faune joue un rôle clef sur le processus de décomposition (Coq *et al.*, 2010, Hättenschwiler *et al.*, 2011, *chapitre 2*, *chapitre 3*) et il apparait donc nécessaire de mieux comprendre les limitations énergétiques et nutritionnelles de la faune saprophage.**

C. Comment prédire les effets des espèces sur la décomposition et le recyclage des nutriments ?

L'un des résultats forts de nos études est la mise en évidence de l'importance du statut en P des litières (concentration, stœchiométrie). Ainsi, le contenu en P des litières est primairement limitant et la variation du statut en P des litières devrait avoir d'importantes conséquences sur la dynamique d'immobilisation /minéralisation du P. A l'heure actuelle, peu d'études ont considéré les relations ente la qualité des litières et la minéralisation du P. Cependant, quelques unes mettent en évidence une forte immobilisation du P au cours de la décomposition en forêt tropicale (Cleveland *et al.*, 2002; Mcgroddy *et al.*, 2004b; Xu *et al.*, 2005), car il est retenu dans la biomasse microbienne. Ainsi, en forêt subtropicale du Japon, Xu et collaborateurs (2005) ont mis en évidence qu'après douze mois de décomposition, les litières de 7 espèces d'arbres présentaient des contenus en P plus élevés que les contenus initiaux, du fait de l'immobilisation du P dans la biomasse microbienne colonisant ces litières. Ce résultat met en évidence que des approches corrélatives reliant les taux de

décomposition aux traits des litières ne sont pas suffisantes pour comprendre les effets des espèces sur le recyclage des nutriments.

Il apparaît que la variation de l'amplitude de la limitation des ressources imposée par le contenu en P des litières n'est pas corrélée avec la variation des taux de décomposition sans fertilisation (Fig. 10). Autrement dit, une espèce décomposant rapidement peut par ailleurs imposer une forte limitation en P et une forte immobilisation de cet élément dans la biomasse microbienne. Ainsi, une décomposition rapide ne signifie pas nécessairement une minéralisation nette importante. L'immobilisation potentielle du P dans la biomasse microbienne devrait avoir d'importantes conséquences pour la disponibilité en nutriments des arbres.

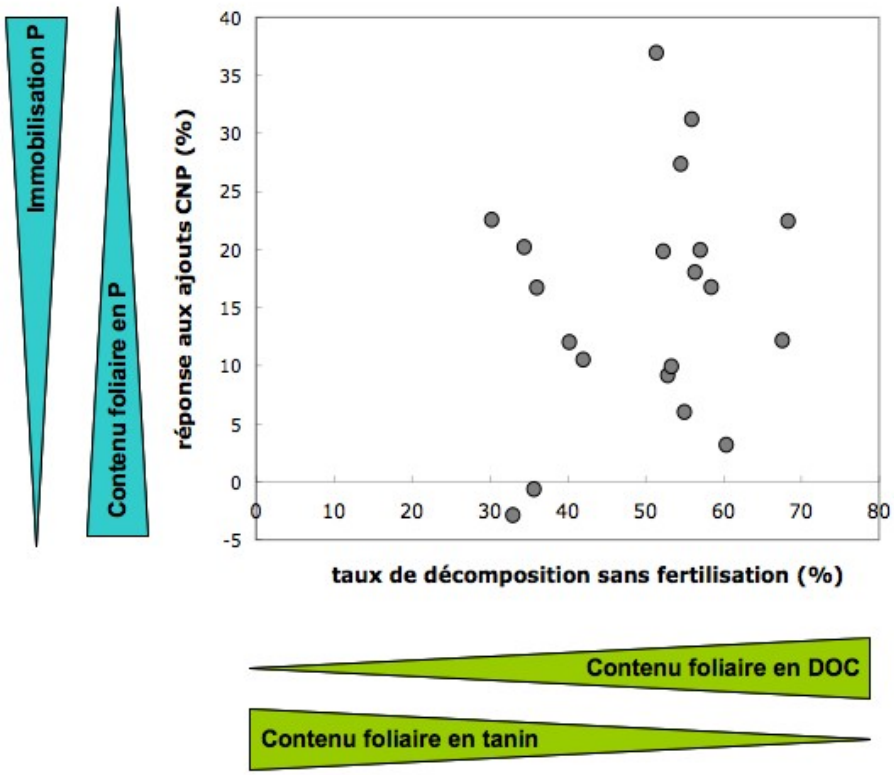

Figure 10: Réponse aux ajouts des ressources CNP en fonction des taux de décomposition des différents substrats (en présence de faune). Les données proviennent de l'expérimentation présentée dans le chapitre 2. La variation des taux de décomposition sans fertilisation était expliquée par les contenus en DOC (carbone organique dissous) et en tanins condensés. La réponse aux ajouts des ressources CNP était corrélée au contenu en P des litières.

II. Des espèces seules aux mélanges des litières : le rôle de la diversité

Dans les *chapitres 3 et 4*, nous avons considéré les effets de la diversité des litières sur la décomposition. Le nombre d'espèces de litières présentes dans les mélanges n'avait pas d'influence sur les taux de décomposition, comme déjà mis en évidence dans la littérature (Wardle *et al.*, 1997; Lecerf *et al.*, 2007; Ball *et al.*, 2008; Jonsson & Wardle, 2008). Le nombre d'espèces en mélanges dans notre étude était relativement bas (au maximum 6 espèces en mélanges, chapitre 4), mais était bien représentatif des mélanges naturels. En effet, à l'échelle du m^2, les mélanges de litières dans notre site d'étude sont composés généralement de 5 à 9 espèces (Sylvain Coq, *communication personnelle*).

Nous avons mis en évidence des interactions entre les différents types de litières (effets non-additifs), pour la plupart synergiques. En effet, les taux de décomposition observés des mélanges étaient généralement plus élevés que ceux prédits à partir des taux de décomposition des espèces seules. A notre connaissance, seulement deux études ont considéré les effets non-additifs des mélanges de litières sur la décomposition en forêt tropicale. Dans l'une d'elles, conduite au Panama, Scherer-Lorenzen et collaborateurs (2007) rapportaient des effets neutres des mélanges, tandis que la seconde étude, conduite dans une forêt de la côte Atlantique brésilienne, rapportait des effets synergiques prédominants (Giesselmann *et al.*, 2010). Etant donné le peu d'études réalisées à ce jour, il semble difficile de replacer les résultats de cette thèse dans le contexte du biome tropical. Cependant, l'amplitude moyenne des effets de mélanges que nous reportons (en moyenne 15 - 20 % de la décomposition totale des mélanges) est représentative d'études conduites dans d'autres biomes (Gartner & Cardon, 2004). Nous montrons dans le chapitre 3 que la présence des détritivores contribue fortement à créer ces effets synergiques dans les mélanges de litières. De plus, nous montrons également que ces effets synergiques dans les mélanges sont renforcés à travers la présence à long terme des espèces d'arbres contribuant à ces mélanges (*chapitre 4*).

Les effets non-additifs des mélanges de litières sont généralement considérés comme difficilement prédictibles, puisqu'ils dépendent largement de combinaisons particulières

d'espèces. Bien que la plupart des mécanismes soient probablement liés à des différences de traits, très peu d'études ont utilisé des mesures continues de diversité fonctionnelle pour expliquer les effets de mélanges (mais voir Hoorens *et al.*, 2003; Meier & Bowman, 2010). Dans ce travail, nous avons cherché à prédire et à comprendre ces effets non–additifs, en prenant en compte des mesures continues de diversité fonctionnelle. Dans le *chapitre 3*, les mélanges de litières ont été choisis de façon à maximiser la gamme de variation de la dissimilarité stœchiométrique (calculée à partir des ratios C:N et N:P des litières). **Nous avons mis en évidence qu'une forte dissimilarité stœchiométrique favorisait des effets synergiques dans les mélanges de litières, en présence de faune.** Ainsi l'association d'espèces ayant des stœchiométries dissimilaires favorise un meilleur équilibre nutritionnel pour la faune saprophage et donc une décomposition plus élevée.

Dans le *chapitre 4*, les mélanges de litières étaient composés à partir d'un plus grand nombre d'espèces, permettant une plus large gamme de diversités chimique (richesse, équitabilité et dissimilarité fonctionnelles). Cependant, aucune des mesures de diversité fonctionnelle utilisées ne permettait d'expliquer les effets non-additifs des mélanges. Avec ces données, nous avions calculé nos indices avec toutes les combinaisons possibles de traits (résultats non présentés dans l'article), y compris avec les traits reliés à la stœchiométrie C:N:P, et il n'apparaissait aucune relation entre les effets de mélanges et les différents indices. Il est assez difficile d'expliquer ces résultats apparemment contradictoires. Cependant, dans le *chapitre 3*, nous avons maximisé notre gradient de diversité fonctionnelle en nous basant sur la stœchiométrie d'un faible nombre d'espèces (6). Au contraire, dans le chapitre 4, nous avions maximisé la diversité chimique en créant 28 mélanges composés à partir de 16 espèces, ce qui devrait augmenter la gamme possible d'éléments chimiques en présence, masquant ainsi le rôle potentiel de certain trait clés.

Aux vues du nombre de jeux de données actuellement publiés sur les effets de la diversité des litières, il serait intéressant d'appliquer ces indices de diversité fonctionnelle pour dégager leur potentiel à prédire les effets non- additifs.

III. Quelles conséquences à l'échelle de l'écosystème?

L'ensemble des résultats obtenus ont permis de mettre en évidence un fort effet des espèces et de leur combinaison, à la fois sur les taux de décomposition, mais aussi sur l'étendue des limitations nutritives. Nos résultats révèlent que la diversité des arbres, de par la qualité de leurs litières, seules ou en mélange, engendre une mosaïque de contraintes nutritionnelles. Bien que la minéralisation nette des éléments n'ait pas été mesurée, cette mosaïque de contraintes devrait moduler la distribution des nutriments disponibles dans le sol ainsi que la structure et le fonctionnement des communautés hétérotrophes du sol. Dans une étude conduite sur le même site, Fanin et collaborateurs (2011) (Cf. *Annexe C*) ont montré que la variabilité de la qualité des apports de litières expliquait largement la variation de la respiration microbienne du sol sous jacent. On peut donc s'attendre à ce que des litières de qualité différente aient un impact sélectif important sur les communautés microbiennes et modulent de ce fait le recyclage des nutriments.

Enfin, ces variations des nutriments disponibles dans le sol et des communautés microbiennes exercent à leur tour des effets « feed-back » sur la croissance des plantes et les communautés végétales (Bezemer *et al.*, 2006; Van Der Heijden *et al.*, 2008). Pour mieux comprendre ces interactions et effets de retour entre plantes et décomposeurs, une caractérisation plus fine des communautés de décomposeurs est cruciale. Au cours de mes travaux de thèse, je me suis concentrée sur la caractérisation chimique des litières en relation avec leur identité taxonomique et le processus de décomposition. Cela a permis d'approfondir notre compréhension du rôle de la diversité végétale, *via* les apports de matière organique morte, sur la décomposition en forêt tropicale humide. Par contre, je n'ai pas évalué comment la diversité des litières et l'ajout expérimental de ressources influencent la composition et la diversité de la communauté des décomposeurs. Approfondir la caractérisation de la diversité fonctionnelle des communautés décomposeurs constitue une importante perspective pour de futures études. Alors que les outils et les approches pour caractériser la diversité fonctionnelle des litières sont relativement bien mis en place, ceux permettant une caractérisation fonctionnelle des détritivores le sont moins et ceux nécessaires à la caractérisation de la diversité fonctionnelle des communautés microbiennes sont encore plus difficiles à mettre en œuvre (Cf. *Annexe C*). Par exemple il semble évident

que les termites et les millepattes, qui constituent une composante importante de la communauté détritivore, ont un fonctionnement différent et subissent très probablement des contraintes nutritives contrastées. Dans de futures études, il serait intéressant de quantifier ces contraintes et d'étudier les comportements de ces différents groupes en fonction d'une qualité de litière diverse et en réponse aux ajouts de nutriments. En ce qui concerne la composante microbienne, une première caractérisation grossière de la structure des communautés utilisant par exemple la méthode des PLFA (caractérisation des acides gras membranaires) pourrait nous éclairer sur l'importance relative de différents groupes de champignons et de bactéries dans notre système d'étude et leurs réponses relatives à des qualités de litières distinctes et des disponibilités de ressources variables. Le projet StoichioDIVERSITY (projet Amazonie phase II) devrait nous apporter quelques éléments sur ces questions dans un avenir proche. Il sera alors intéressant d'interpréter les résultats acquis au cours de ma thèse à la lumière de ces nouvelles données.

Enfin, une perspective à plus long terme serait de lancer des études comparatives à travers des forêts tropicales humides différentes. Des ajouts expérimentaux de ressources en C, N, et P combinées sont encore très rares d'une manière générale et surtout pour les écosystèmes tropicaux. En incluant dans ce type d'étude des forêts tropicales sur des sols différents (en termes de disponibilité en nutriments) et en utilisant différentes formes de composés carbonés, de telles études conduites de manière comparative pourraient nous apporter des réponses importantes à des questions fondamentales sur l'importance du rôle de la diversité en interaction avec la disponibilité en ressource pour le fonctionnement de ces écosystèmes.

Annexe A

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

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Abstract

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 (1) litter traits are a mere legacy of live leaf traits (2) nitrogen (N) and lignin are the key litter traits controlling decomposition, and (3) that 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.

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

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 (Millenium Ecosystem Assessment, 2005; IPCC 2007). Tropical forests are often cast in the spotlight as they stand out as highly significant reservoir 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 carbon (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 of 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 (Gonzalez & 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 to, 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 of how plants and decomposers interactively influence biogeochemical cycling. We aim to revisit the commonly held views that (1) plant leaf litter traits relevant for decomposition are simply a legacy of live plant functional traits with an accidental influence on decomposition, (2) litter nitrogen (N) and lignin as the two commonly used traits for model parameterization predict litter decomposition in tropical rainforests well, and (3) 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-year average, 1995-2005) with a drier period, usually < 100 mm per month, from August to November (10-year 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-year average, 1995-2005). Soils are nutrient-impoverished acrisols (FAO 1998) developed over a Precambrian metamorphic formation called the Bonidoro-series, with a pH of about 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 a high stoichiometric and carbon 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 for 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 fiber 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 a plant-soil feedback where plants at the quick end of the leaf economics spectrum produce rapidly decomposing nutrient-rich litter that tends to maintain a 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 highest source of variation among plant species remained within-site differences (Ordoñez *et al.,* 2009).

With about 23 mg total P kg^{-1} 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 to 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 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 a 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 the 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

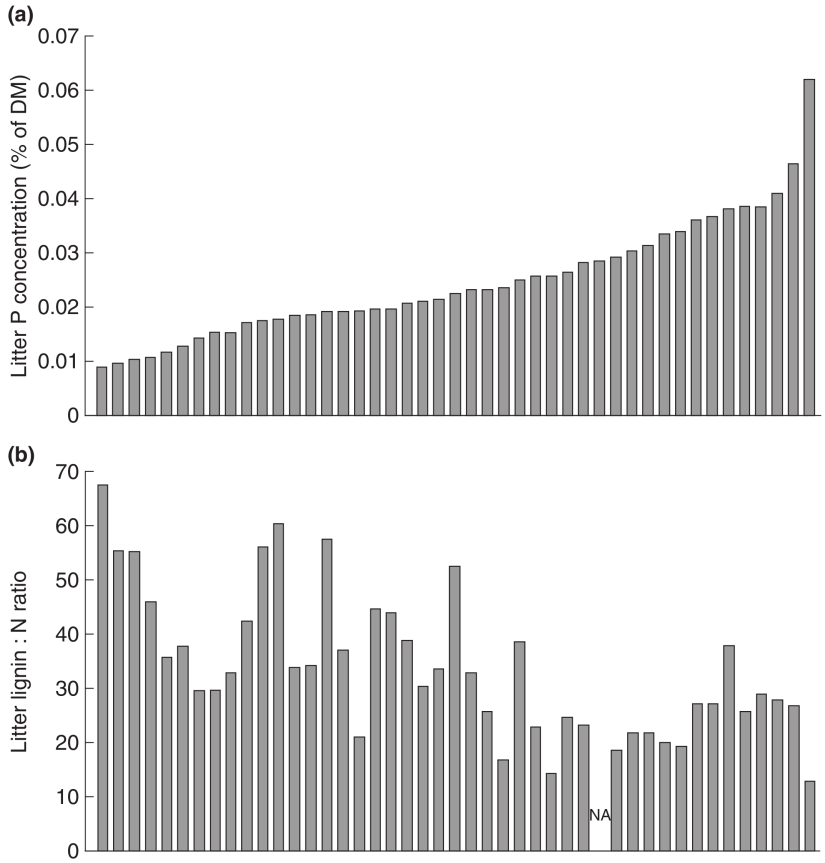

Figure 1: Litter phosphorus concentrations (top panel) and lignin/N ratios (bottom panel) from 45 co-occurring Amazonian rainforest trees (data from Hättenschwiler *et al.,* 2008). Data are presented in the order of increasing litter P concentration with the respective species-specific lignin/N ratio underneath (see Hättenschwiler *et al.,* 2008 for species identity).

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 litter were significantly correlated (r^2 = 0.55, Hättenschwiler *et al.*, 2008). Moreover, a lower average N resorption efficiency of 40 ± 13%, and litter N concentrations that remained for all but four species above the threshold of 0.7% indicative of complete N 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.

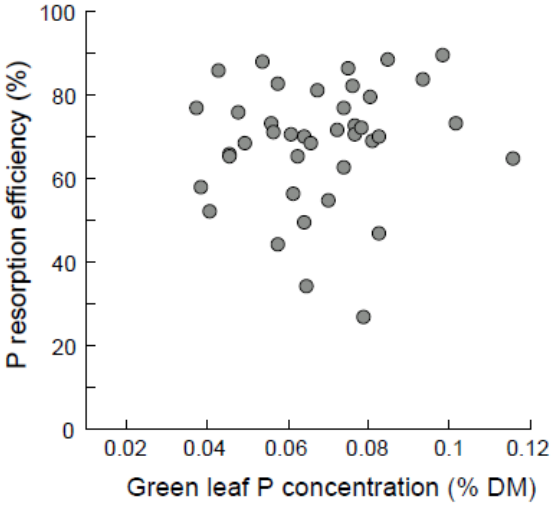

Figure 2: Phosphorus resorption efficiency as a function of green leaf P concentration of the same 45 co-occurring Amazonian rainforest trees presented in Fig. 1 (data from Hättenschwiler *et al.*, 2008). Phosphorus resorption efficiency was estimated on a unit lignin basis (i.e. total green leaf P and 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).

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 play 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 a 18.4-fold range in decomposition rates attributable to plant species-specific differences in litter quality compared to 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 correlate well with the variability in

decomposition rates (e.g. Melillo *et al.,* 1982; Taylor *et al.,* 1989; Moore *et al.,* 1999) and is 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 on 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 the 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 for 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 a rather rapid exploitation of this resource by soil microorganisms, and thus a more rapid decomposition of relatively P-rich litter, as observed in P-limited Hawaiian montane tropical forests (Hobbie & Vitousek, 2000).

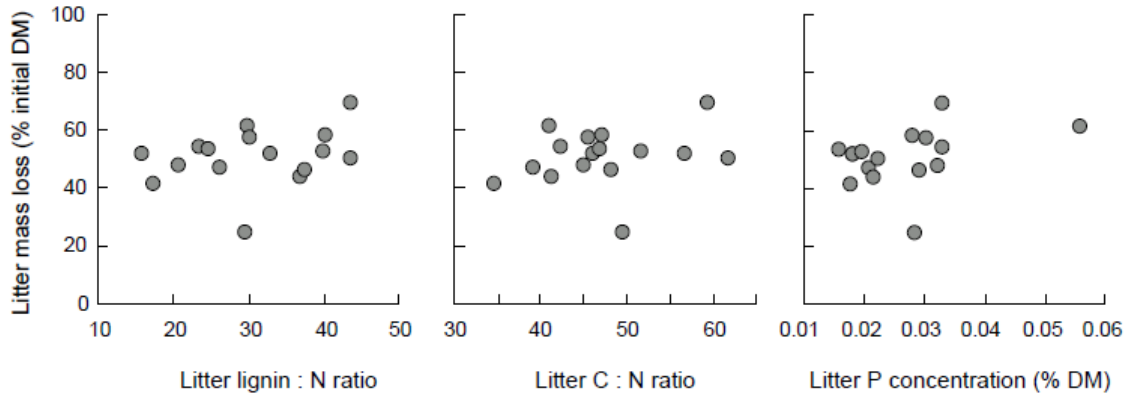

Figure 3: Litter mass loss of 16 Amazonian rainforest tree species as a function of initial litter lignin : N ratio, C : N ratio, and P concentration (data from Coq et al. 2010). Each data point represents the average of n = 4 fine mesh (0.068 mm) litterbags per species exposed in the undisturbed rainforest for 312 days. 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).

Why do the commonly used litter traits predict decomposition so poorly in the studied lowland Amazonian forest? Given that 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, 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 NCSs and phenolics, which occur in comparatively low concentrations, correlated positively with litter mass loss (Fig. 4). According to our protocol, NSCs consisted of C6-

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

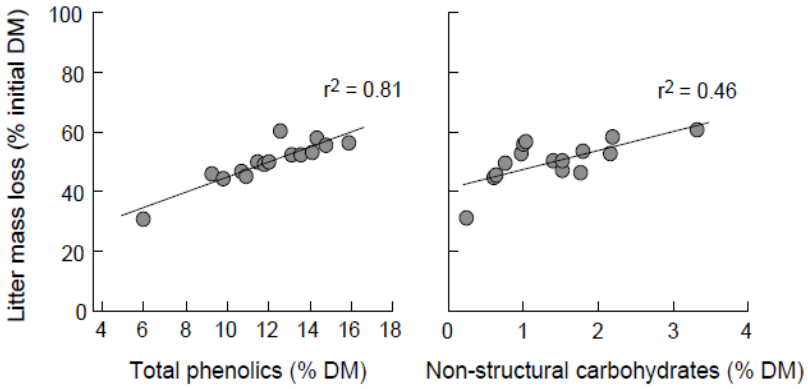

Figure 4: Litter mass loss of four single litter species and all possible combinations thereof as a function of initial litter concentrations of total phenolics and non-structural carbohydrates (NSC) after 204 days of field exposure (data from Hättenschwiler & Bracht Jørgensen 2010). Each data point 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) of the totally 15 different litter treatments). Simple linear regressions were significant at *P* < 0.001 (total phenolics) and at *P* = 0.006 (NSC).

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 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 wronlgy 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 underlying 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%, or 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 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 like 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, 2005) 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 dominantly used 1-mm mesh width, for example, prevents all macrofauna (macroarthropods and earthworms) from entering, but allows access of a large part 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 (mesh sizes of litter bags) or chemical suppression (naphtalene) across different biomes (Anderson *et al.,* 1983; Gonzalez & Seastedt, 2001; Heneghan *et al.,* 1999; Wall *et al.,* 2008; Yang & Chen, 2009). The latter three studies used litterbags of ≤ 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 presence of fauna (2-mm mesh bags) compared with the 45% mass loss in its absence (0.l15-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 (2009)'s study compared to 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) exposed single-species litter from a range of different species. The contribution of fauna to decomposition depended strongly on 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 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).

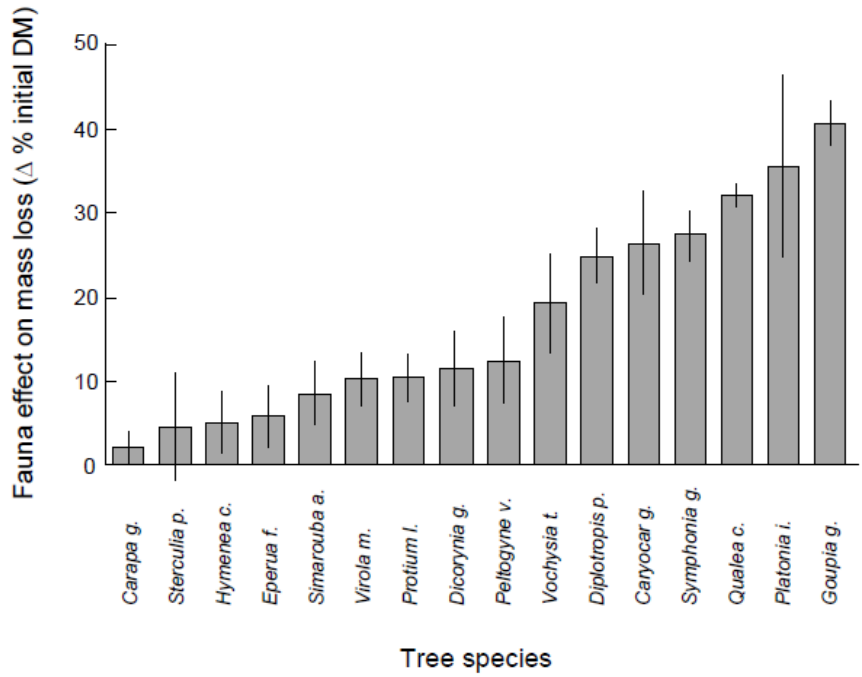

Figure 5 : Fauna effect on mass loss of litter from 16 different Amazonian tree species after field exposure of 312 days (mean ± SE, n =4, data from Coq et al. 2010). The fauna effect is defined as the difference in per cent mass loss between large mesh width litterbags (8 mm) and small mesh width litterbags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

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 (Wall *et al.*, 2008; Powers *et al.*, 2009). The fauna effect, however, depends on 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 ≤ 2 mm and/or the use of 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°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, and thus decomposition rate, with a temperature increase, for example, from 15°C to 25°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 likely quite rich in NSCs, thus, providing a more favourable C quality compared to 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 biogeographic regions of varying tree species composition and soil types, but relatively high annual precipitation, the average mass loss of litter from native tree species after 312 d of field exposure was 67 ± 5% which surprisingly is identical to the average measured across the 16

species at our study site (67 ± 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 particularly 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 moderate (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°C in the tropical rainforest compared with 7.2°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 2 lower compared with *Fagus sylvatica*, the most recalcitrant litter type in European temperate forests.

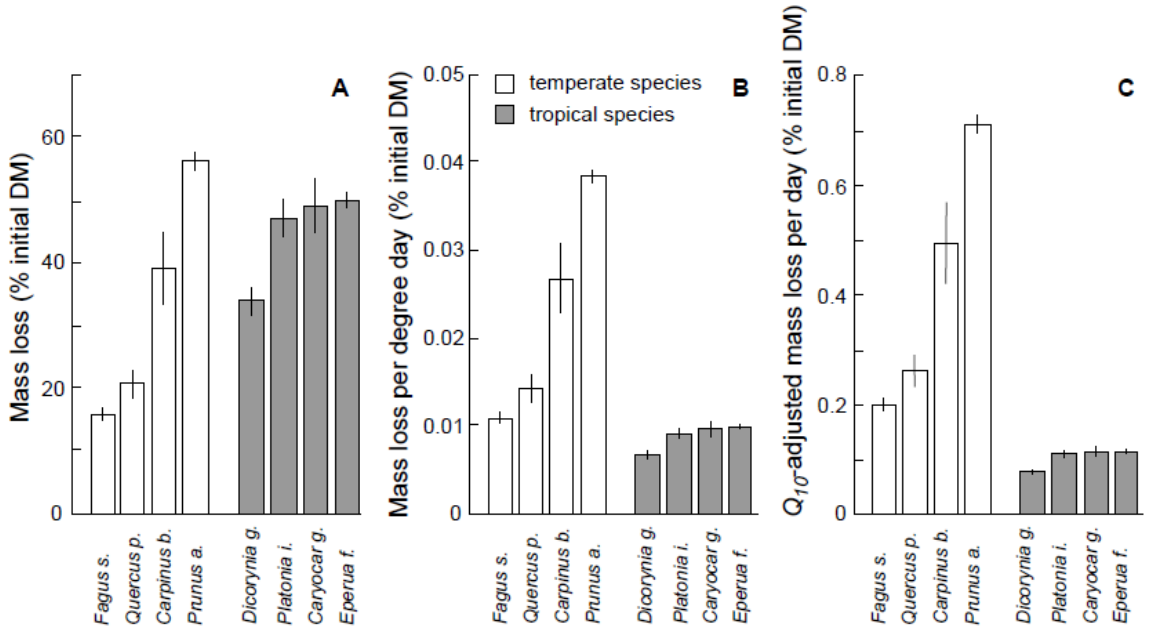

Figure 6: Litter mass loss of four European temperate forest tree species (*Fagus sylvatica, Quercus petraea, Carpinus betulus, Prunus avium,* data from Hättenschwiler & Gasser 2005) and four Amazonian trropical rainforest tree species (*Dicorynia guianensis, Platonia insignis, Caryocar glabrum, Eperua falcata,* data from Hättenschwiler & Bracht Jørgensen 2010). Litter from both sets of species decomposed in their undisturbed mature forest of origin over exactly the same period of time of 204 days during the humid part of the year (November to June). The same experimental setup of field microcosms with open bottom and sides covered with 0.5 mm mesh and 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 ± SE] for temperate and tropical species, respectively; see references above for experimental details and site descriptions). A: Total mass loss in per cent of initial dry mass after 204 days 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 duration). Temperature has been measured continuously at 3-hour 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 duration was 7.2 °C and 24.8 °C with 1463 and 5083 degree days in the temperate and the tropical experiment, 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 to 2.94 in the tropical forest (Q_{10} values are taken from the broad comparison across different biomes published by Zheng *et al.*, 2009).

These results suggest that the litter 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 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 (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 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 leading to substantial errors in estimates of tropical decomposition rates.

Table 1 Comparison of mass loss rates from litter bag decomposition studies carried out in primary tropical rainforests around the world using local canopy tree litters. Mass loss (ML) for 365 days and for the equivalent duration at our study site of 312 days (d) are 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).

Reference	Location	Soils[1]	Rainfall[2] (mm); dry season	Litter type species	Duration (d)	Mesh (mm)	k (a^{-1})	Mass $loss_{365}$ (%)	Mass $loss_{312}$ (%)
Our study site (Coq *et al.*, 2010)	Neotropic Paracou French Guiana	Acrisols	2575; August–November	*Carapa procera*	312	8 × 8			52.2
				Caryocar glabrum					73.3
				Dicorynia guianensis					52.5
				Diplotropis purpurea					73.5
				Eperua falcata					67.1
				Goupia glabra					92.9
				Hymenaea courbaril					69.2
				Peltogyne venosa					65.0
				Platonia insignis					83.5
				Protium sagotianum					53.9
				Qualea rosea					82.9
				Simarouba amara					57.5
				Sterculia pruriens					57.6
				Symphonia sp.					77.7
				Virola surinamensis					82.3
				Vochysia tomentosa					37.3
				Mean (of 16 species)					**67.4**
Cleveland *et al.* (2006)	Neotropic Osa Peninsula Costa Rica	Ultisols	> 5000; January–March	*Brosimum utile*	300	1 × 1	2.82	94.0	91.0
González & Seastedt (2001)	Neotropic Luquillo Experimental Forest Puerto Rico	Oxisols	3524; no dry season	*Cecropia scheberiana* 1.8 × 1.6	528 1.47	76.9	71.4		
Santiago (2010)	Neotropic San Lorenzo National Park Panama	Histosols	3100; January–April	**Mean (of 11 species)**	744	1 × 1	0.71	**50.6**	**45.3**
Wieder *et al.* (2009)	Neotropic Golfo Dulce Forest Reserve Osa Peninsula, Costa Rica	Ultisols	> 5000; December–April	Local mixture	230	1 × 1	1.93	85.5	80.8
				Brosimum utile			1.31	73.0	67.4
				Cecropia obtusifolia			0.96	61.7	56.0
				Ceiba pentandara			2.58	92.4	89.0
				Huberodendron allenii			1.62	80.2	75.0
				Hyeronima alchorneoides			0.86	57.7	52.1
				Inga spp.			1.62	80.2	75.0
				Manilikara staminodella			0.99	62.8	57.1
				Pouteria lecythidicarpa			1.11	67.0	61.3
				Qualea paraensis			1.13	67.7	61.9
				Schizolobium parahyba			3.24	96.1	93.7
				Symphonia globulifera			2.13	88.1	83.8
				Mean (of 11 species)				**75.2**	**70.2**

Table 1 (continued)

Reference	Location	Soils[1]	Rainfall[2] (mm); dry season	Litter type species	Duration (d)	Mesh (mm)	k (a^{-1})	Mass $loss_{365}$ (%)	Mass $loss_{312}$ (%)
Anderson *et al.* (1983)[3]	Indo-Malaya Gunung Mulu National Park Sarawak, Malaysia	Peaty podsols Red-yellow podsols Humus podsols, 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	**Minimum value (40 sp.)** **Maximum value (40 sp.)**	168	2 × 2	0.67 4.85	**48.8** **99.2**	**43.6** **98.4**
Rogers (2002)[4]	Australasia Oomsis Forest, Morobe Papua, New Guinea	Chromic Luvisols (Schist-derived)	3000; no dry season	*Pometia pinnata* *Celtis kajewskii* *Dysoxylum caulostachyum* **Mean (of 3 species)**	84	1 × 1	1.17 2.12 2.22	69.0 88.0 89.1 **82.0**	63.2 83.7 85.0 **77.3**
Chuyong *et al.* (2002)[3]	Afrotropic Korup National Park Cameroon	Sandy, nutrient-poor, strongly acidic	5060; December–February	*Berlinia bracteosa* *Didelotia africana* *Microberlinia bisulcata* *Tetraberlinia bifoliolata* *Cola verticillata* *Oubanguia alata* *Strephonema pseudocola* **Mean (of 7 species)**	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 **83.4**	88.3 56.4 70.5 66.3 88.4 94.6 89.5 **79.1**

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.

[1]The soil description uses inconsistent nomenclature but summarizes the details as provided by the authors.

[2]Rainfall refers to total annual precipitation as estimated from long-term means.

[3]k values in the original publications were calculated for a t in months and are expressed here for a t in years.

[4]Selectively logged 35 yr ago.

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 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 inhibiting 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 Wurzburger & Hendrick (2009), with the latter study 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; Leigh *et al.,* 2009; Atul-Nayyar *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 (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 by 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, 1996; 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 N2-fixing) (Newberry *et al.,* 1988; Alexander, 1989), and tend to dominate 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 most likely related to a 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 of 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 number 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 a detailed characterization of 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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Annexe B

Does variability in litter quality determine soil microbial respiration in an Amazonian rainforest?

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Abstract

Tree species-rich tropical rainforests are characterized by a highly variable quality of leaf litter input to the soil at small spatial scales. This diverse plant litter is a major source of energy and nutrients for soil microorganisms, particularly in rainforests developed on old and nutrient impoverished soils. Here we tested the hypothesis that the variability in leaf litter quality produced by a highly diverse tree community determines the spatial variability of the microbial respiration process in the underlying soil. We analyzed a total of 225 litter-soil pairs from an undisturbed Amazonian rainforest in French Guiana using a hierarchical sampling design. The microbial respiration process was assessed using substrate-induced respiration (SIR) and compared to a wide range of quality parameters of the associated litter layer (litter nutrients, carbon forms, stoichiometry, litter mass and pH). The results show that the variability of both litter quality and SIR rates was more important at large than at small scales. SIR rates varied between 1.1 and 4.0 μg g-1 h-1 and were significantly correlated with litter layer quality (up to 50% of the variability explained by the best mixed linear model). Total litter P content was the individual most important factor explaining the observed spatial variation in soil SIR, with higher rates associated to high litter P. SIR rates also correlated positively with total litter N content and with increasing proportions of labile C compounds. However, contrary to our expectation, SIR rates were not related to litter stoichiometry. These data suggest that in the studied Amazonian rainforest, tree canopy composition is an important driver of the microbial respiration process via leaf litter fall, resulting in potentially strong plant-soil feedbacks.

Key-words: Carbon forms, French Guiana, litter quality, microbial respiration process, nitrogen, phosphorus, stoichiometry.

1. Introduction

Forests account for 47% of the total storage capacity of carbon (C) in terrestrial ecosystems worldwide (Melillo *et al.,* 1993; Malhi *et al.,* 2002; IPCC, 2007), with more than two thirds of which contained in soils (Malhi *et al.,* 1999; Peng *et al.,* 2008). Tropical forest ecosystems play a key role in the global C cycle (Philipps *et al.,* 1998; Malhi &Grace, 2000; Grace *et al.,* 2001; Luyssaert *et al.,* 2008), but the regulation of C storage and soil C fluxes is subject to important uncertainties (Clark, 2002; Loescher *et al.,* 2003; Saleska *et al.,* 2003). Whether or not carbon is sequestered in forest ecosystems depends on the often small difference between photosynthetic carbon fixation and ecosystem respiration, with soil respiration representing 40 to 95% of the total ecosystem respiration (Granier *et al.,* 2000; Janssens *et al.,* 2001; Chambers *et al.,* 2004; Epron *et al.,* 2004; Yuste *et al.,* 2005). Total soil respiration is essentially the sum of root respiration and associated rhizosphere organisms (autotrophic respiration) and microbial litter decomposition and mineralization of soil organic matter (heterotrophic respiration) (Hanson *et al.,* 2000; Kuzyakov, 2006). Understanding the control factors over soil respiration is particularly important because even small changes in soil respiration can determine whether forest ecosystems act as a source or a sink of C (Subke *et al.,* 2006).

Factors controlling heterotrophic soil respiration and determining its temporal and spatial variation at large scales are mostly of abiotic nature (e.g soil water content, soil texture, temperature). Their impact on soil respiration is reasonably well understood for a variety of forest ecosystems (Hanson *et al.,* 1993; Davidson *et al.,* 1998; Rey *et al.,* 2002; Khomik *et al.,* 2006; Bonal *et al.,* 2008; Adachi *et al.,* 2009). However at smaller spatial scales, soil respiration varies considerably beyond environmental drivers (Epron *et al.,* 2006; Katayama *et al.,* 2009; Martin & Bolstad, 2009). This residual variation appears to be related to biotic rather than abiotic factors, but biotic control over soil respiration is only poorly understood (Grayston *et al.,* 2001; see also Hooper *et al.,* 2000 for a review), especially in undisturbed forests (Epron *et al.,* 2006).

Among these biotic factors, the vegetation is of overriding importance through the production of quantitatively and qualitatively different resource inputs via rhizodeposition and litter production (Binkley & Giardina, 1998; Epron *et al.,* 2004; Wardle *et al.,* 2004). Plant

litter represents a key source of food for the complex and highly diverse heterotrophic soil food webs, with mostly microorganisms having the enzymatic capacity for the breakdown of complex organic molecules and the mineralization of nutrients (Swift *et al.,* 1979; Cadisch & Giller, 1997). For their growth and reproduction, heterotrophic soil microorganisms depend themselves on the energy and nutrients provided through plant litter, but they also provide nutrients in mineral form for plant uptake. As a critical resource, nitrogen (N) has often been found to limit soil microbial processes (e.g. Chapman *et al.,* 2006; Craine *et al.,* 2007), especially in temperate ecosystems that tend to be N-limited (Rennenberg *et al.,* 2009). In contrast, tropical ecosystems that typically developed on old and nutrient-impoverished soils are considered to be rather phosphorus (P) limited (Vitousek *et al.,* 2010). However, perhaps more than the absolute amounts of nutrients, their relative abundance in relation to C may be important for the growth of individuals, ecosystem productivity and trophic interactions (Sterner & Elser, 2002). The theory of ecological stoichiometry (Sterner & Elser, 2002) predicts important constraints of C:nutrient ratios on decomposer communities because they have distinctively narrower C:nutrient ratios than the litter they consume (Cleveland & Liptzin, 2007; Martinson *et al.,* 2008).

Large variation in litter quality and stoichiometry has been observed among tropical tree species at regional (Townsend *et al.,* 2007) and small local scales (Hättenschwiler *et al.,* 2008). Such high interspecific variation in litter quality combined with the high tree species diversity in tropical forests results in a spatially highly variable organic matter input to the soil. Does a heterogeneous plant litter input to the soil explain some of the spatial variability of microbial respiration in the underlying soil? For answering this question the spatial scale considered matters. Generally, the degree of plant control on soil biota and microbial processes is thought to be highly scale dependent (see Hooper *et al.,* 2000 for review). At a small scale of only a few meters, the composition of leaf litter, and thus its quality should be more similar than at larger scales of a few hundreds of meters, because of greater overlap of individual trees contributing to the litter pool on the forest floor. With increasing spatial scales, the composition of the litter producing tree community changes in response to differences in topography, soil texture and chemistry, and landscape dynamics (John *et al.,* 2007) that is consequently creating higher variability in litter quality input to the soil (Townsend *et al.,* 2008). Recent studies in tropical forest ecosystems reported wide variations

in litter quality-driven decomposition rates (Wieder *et al.*, 2009; Coq *et al.*, 2010; Hättenschwiler & Bracht-Jørgensen, 2010) and in soil microbial community structure (Carney & Matson, 2006) at small spatial scales. However, to our knowledge, the relationship between spatial variation in plant litter input and soil microbial respiration has not explicitly been tested so far.

With this study we aimed to test the hypothesis that the variation in leaf litter quality produced by a highly diverse tree community determines, at least in part, the spatial variability of the microbial respiration process in the underlying soil of the tropical rainforest at Paracou, French Guiana. We anticipated a relatively strong control of litter element and carbon forms on soil microbial respiration process because, in the studied nutrient-poor system, plant litter constitutes a major source of energy and nutrients for soil organisms. Based on the predictions of ecological stoichiometry, we expected a particularly important influence of litter stoichiometry. We also hypothesized a lower variability of leaf litter traits and associated microbial respiration process at small spatial scales compared to larger spatial scales. We tested these hypotheses using a nested sampling design in order to account for the variability of leaf litter quality at different spatial scales and to determine how this variability is partitioned among two hierarchical levels for a better understanding of ecosystem processes and factors that drive these processes (Schneider, 2001; Urban, 2005).

2. Materials and Methods

2.1. Study site

The study site is located within the undisturbed Amazonian rainforest of Paracou near Sinnamary, French Guiana (5°15'N, 53°'W). The mean annual air temperature is 25.5 °C (10-year average, 1995-2005) with only slight intra annual variations. Total annual rainfall is approximately 2575 mm (10-year average, 1995-2005), with two distinct rainy seasons (a moderate one from December to February and a stronger one from April to July) with an associated range in relative air humidity between 70 and 90 % (Bonal *et al.*, 2008). Tree species richness is around 150 species per hectare with a mean density of 620 individual trees ha^{-1} (individuals of a diameter > 0.1 m at breast height, Gourlet-Fleury & Houllier, 2000). The

average tree height is about 35 m. Soils in the study area are classified as acrisol (FAO 1998) developed over a Precambrian metamorphic formation called the Bonidoro series with a mean pH of 4.7 in the top soil. Soil texture, major (C, N, P) and microelements (Al, Fe, K, Mg, Mn) are listed in the Table 1 (analyses realized by the Laboratoire d'Analyse des Sols, INRA Arras, France, using standard methods).

Table 1. Soil texture (a) and elemental composition (b) of the five studied blocks (A, B, C, D, E) in the undisturbed tropical rainforest at Paracou, French Guiana.

(a) Soil texture†‡	**A**	**B**	**C**	**D**	**E**
Clay (%)	16.2 ± 2.2^{b}	15.6 ± 3.3^{b}	20.9 ± 1.7^{a}	21.7 ± 2.3^{a}	24.1 ± 1.6^{a}
Fine silt (%)	3.2 ± 0.4^{c}	3.0 ± 0.8^{c}	3.4 ± 0.7^{c}	4.6 ± 0.5^{b}	7.0 ± 1.0^{a}
Coarse silt (%)	2.2 ± 0.2^{a}	1.4 ± 0.4^{b}	2.1 ± 0.3^{a}	1.9 ± 0.4^{a}	2.2 ± 0.3^{a}
Fine sand (%)	23.5 ± 2.5^{a}	11.4 ± 1.9^{b}	11.7 ± 1.1^{b}	12.6 ± 1.2^{b}	10.3 ± 1.0^{b}
Coarse sand (%)	54.8 ± 3.5^{c}	68.5 ± 5.7^{a}	61.9 ± 3.6^{b}	59.2 ± 2.9^{c}	56.4 ± 3.0^{c}

(b) Soil elements†‡	**A**	**B**	**C**	**D**	**E**
C (%DM)	2.06 ± 0.63^{bc}	1.87 ± 0.40^{c}	2.30 ± 0.45^{b}	2.16 ± 0.60^{bc}	2.67 ± 0.27^{a}
N (%DM)	0.130 ± 0.030^{c}	0.133 ± 0.026^{c}	0.164 ± 0.030^{ab}	0.149 ± 0.038^{bc}	0.180 ± 0.016^{a}
P (%DM)	0.008 ± 0.002^{c}	0.008 ± 0.002^{c}	0.011 ± 0.003^{b}	0.011 ± 0.002^{b}	0.013 ± 0.001^{a}
K (g /100g)	0.043 ± 0.005^{c}	0.037 ± 0.007^{c}	0.042 ± 0.003^{c}	0.053 ± 0.005^{b}	0.072 ± 0.012^{a}
Fe (g /100g)	1.90 ± 0.26^{b}	1.65 ± 0.38^{bc}	2.37 ± 0.43^{b}	1.25 ± 0.12^{c}	3.02 ± 0.32^{a}
Al (g /100g)	2.5 ± 0.26^{d}	3.46 ± 0.70^{c}	4.42 ± 0.57^{b}	4.16 ± 0.42^{b}	6.79 ± 0.53^{a}
Mn (g /100g)	0.27 ± 0.05^{b}	0.29 ± 0.05^{b}	0.49 ± 0.12^{a}	0.14 ± 0.07^{c}	0.23 ± 0.28^{b}
Mg (g /100g)	<0.02^{b}	<0.02^{b}	<0.02^{b}	<0.02^{b}	0.027 ± 0.003^{a}

†Soils were collected to 8 cm depth. Soil analyses were done dried and sieved soil (2 mm).
‡Each value represents the average ± SD (n = 9 per block for soil texture, K, Fe, Al, Mn and Mg and n = 45 for C, N and P). Different letters indicate significant differences between blocks (P < 0.05, n = 225, decreasing order, Tukey-HSD tests).

2.2. Sampling design and data collection

A total of five blocks, each of which measuring approximately 3000 m^2, of rather homogeneous flat topography were defined within a 2.5 ha zone. The blocks had been chosen to account for the typical natural variability in tree canopy composition in this species-rich tropical forest with often only one individual tree per hectare of most species, while keeping climatic conditions identical, topography and soil characteristics essentially the same. Within each of the five blocks, we nested nine plots of 5 x 5 m each, and, within each plot, five litter samples together with the underlying soil were taken randomly along one plot diagonal, resulting in a total of 225 couples of litter-soil samples (5 blocks x 9 plots x 5 samples). This nested design allowed comparing the litter variability at large (blocks) and small (plots within blocks) scales. Litter was collected manually using a 0.3 x 0.3 m frame placed on the forest floor. The underlying soil was sampled in the center of the frame using a stainless steel cylinder (diameter of 0.05 m) to a depth of 0.08 m. In the laboratory, all litter samples were sorted in order to remove fruits, seeds and roots, cut into pieces of about 0.02 m using scissors, homogenized, dried at 65°C, and weighed to determine litter dry mass. All soil samples were air-dried, sieved through a 2 mm sieve in order to remove roots and stones and homogenized. All sampling was done from 31 January to 3 February 2009 during the wet season, approximately two months after peak litter fall (Bonal *et al.*, 2008).

2.3. Litter quality and soil characteristics

Litter pH, total carbon, nitrogen and phosphorus, water soluble compounds (WSC), hemicellulose, cellulose, lignin, and condensed tannins were analyzed using standard methods. Except for the pH (whole pieces of litter), all chemical analysis were performed on ground subsamples to obtain a uniform particle size of about 1 mm (Cyclotech Sample Mill, Tecator, Höganäs, Sweden). Carbon and nitrogen concentrations were measured using a CHN elemental analyser (Flash EA1112 Series, ThermoFinnigan, Milan, Italy). For P measurements, 2 ml of H_2SO_4 36 N and 3 ml of H_2O_2 were added to a 25 mg sample of ground leaf litter and heated at 360°C for 4 h. After this mineralization step, P concentration was measured colorimetrically with an autoanalyser (Evolution II, Alliance Instruments,

Frépillon, France) using the molybdenum blue method (Grimshaw et al., 1989). Total soil carbon, nitrogen and phosphorus were analysed using the methods described above but with larger subsamples of ground material (80 mg and 150 mg for CN and P analyses respectively). Water soluble compounds, hemicellulose, cellulose and lignin were determined according to the Van Soest extraction protocol (Van Soest & Wine, 1967) using a fiber analyser (Fibersac 24, Ankom, Macedon, NJ, USA). This method consists to measure the various plant tissue constituents by sequential extraction with neutral detergent, acid detergent, and sulfuric acid (76 %). Condensed tannins were determined by spectrophotometry using the butanol-HCl method (Porter, 1986; modified by Waterman &Mole, 1994). Condensed tannins were extracted with ultrasound from a 5 mg subsample in 5 ml of acetone-water solvent (70-30 %). After this extraction step, 1 ml of supernatant was collected and mixed with 6 ml of butanol-HCl solution and 0.2 ml of ferric reagent ($FeNH_4(SO_4)_2$,12 H_2O). The optical density of each sample was measured at a wavelength of 550 nm with a spectrophotometer (ThermoSpectronic type Helios Gamma, Helios, England) using catechin as standard. The pH was measured from 150 ± 15 mm^3 (1 ± 0.1 g) leaf litter in 1200 mm^3 deionized water (i.e. volume ratio 1:8) according to Cornelissen *et al.,* (2006). The mixtures were stirred for 45 min at 250 rpm and their pH was measured using a probe (pH-vision datalogger 6091, Jenco electronics LTD, San Diego, USA) connected to a pH-meter of the same brand. Soil pH was measured as described above using a 2 g soil subsample.

2.4. Soil microbial respiration process

The substrate induced respiration (SIR) represents the state of the enzyme pool involved in respiration (i.e. of the heterotrophic microbial community) at the time of sampling. It was used as an indicator of the soil microbial functioning (we use the term "microbial respiration process" throughout the paper), as previously described (Pinay *2.2.* 2007; Fromin *2.2.* 2010). In that context, SIR is considered more relevant than actual in situ soil respiration, for which variations can reflect short-term variations in the environmental conditions. Variations in SIR rates also reflect modifications of the microbial functioning due to differences in abundance and/or composition of the heterotrophic microbial community.

Soil SIR was measured according to Beare *et al.* (1990). For each sample, 10 g of soil (dry weight) were placed in a sealed plasma flask of 150 ml. A solution of glucose (a total of 1.5 mg C per g of dry soil) was added to reach 80 % of field capacity. The flasks were incubated at 25° for 6 h, a time span that is considered as short enough to avoid de novo enzyme synthesis. Two 200 µl air samples from the headspace of each flask were analysed after 2 and 6 h incubation for CO_2 concentration with a gas chromatograph using a catharometer (VARIAN GC 4900; Varian, Walnut Creek, USA). The amount of CO_2 released during this time allowed to calculate SIR expressed in µg of C-CO_2 per g of soil per hour.

2.5. Data analysis

Statistical models considered the hierarchical data structure with two levels: the forest stand being represented by 3rd-order blocks and 2nd-order plots nested within blocks. Within each of the five selected blocks, we nested nine replicate plots, and each plots included five replicate litter-soil pairs. Normality of the distribution of data was assessed for all variables by Shapiro-Wilkinson's test and the homogeneity of variance by the Fisher (F) test. When data were not normally distributed, transformations of variables were performed in order to meet the assumptions before any further statistical tests. Nested ANOVA was used to test for differences in litter quality and SIR among blocks and among plots within blocks followed by a post-hoc test of Tukey-HSD (α = 0.05). To examine the importance of scale in understanding sources of variation in soil microbial respiration process, the coefficient of variance (CV) was either calculated based on individual samples within plots at the scale of plots within blocks, or based on the means within plots at the scale of blocks. A standardized principal component analysis (PCA) was used to explore the pattern of relationships among variables of litter quality. The PCA was run using all litter variables, namely total litter mass per unit ground area (g m^{-2}), litter pH, and leaf litter C, N, P, WSC, hemicellulose, cellulose, lignin, and condensed tannins concentrations. An intra-class analysis was performed to visualize the spatial position of the different blocks by calculating the barycenter over the representation of samples per block. Linear Mixed Model with nested grouping factors (for R package "nlme" see Pinheiro *et al.*, 2007; Bates, 2010) was used to assess the effects of individual litter quality traits (expressed as amounts of compounds

per unit ground area) on SIR rates. Blocks and nested plots were considered as random factors while litter nutrients, stoichiometry and carbon forms were used as fixed factors. Three different models were then fitted to describe the relationships between significant litter quality traits (using litter nutrients and carbon only, carbon forms only, and finally the combination of litter nutrients and carbon forms) and SIR rates. Levels of significance are indicated as * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$). All statistical tests were performed with the R software (version 2.11.1).

3. Results

3.1. Variability of soil SIR

SIR varied by almost a factor of 4 between the lowest (1.1 $\mu g\ g^{-1}\ h^{-1}$) and the highest (4.0 $\mu g\ g^{-1}\ h^{-1}$) measured rates. SIR rates differed significantly among the five blocks (Fig. 1a). Block B showed the overall lowest SIR (values ranging from 1.1 to 2.5 $\mu g\ g^{-1}\ h^{-1}$) whereas blocks D and E exhibited the highest SIR on average (values between 1.3 to 4.0 $\mu g\ g^{-1}\ h^{-1}$). The plots within blocks also showed significant differences in SIR, except of block E (Fig. 1b). The variability of SIR was greater among blocks (coefficient of variation CV = 26 %) than among plots within blocks (CV = 17 %).

3.2. Variability of litter layer quality

Clear and significant differences for most of the measured litter traits were observed among the five blocks (Table 2). Total C ($F = 35.6^{***}$) and N ($F = 26.5^{***}$) concentrations were significantly different among blocks, and differed also among plots within blocks ($F = 5.0^{***}$ and $F = 4.0^{***}$ respectively). Block B showed the lowest C (mean 38.5 %) and N concentrations (mean 1.06 %) compared to the other blocks. P concentration was only slightly different among blocks ($F = 2.8^{*}$) but varied considerably with a distinctly higher CV (36 %) compared to C (17 %) or N (18 %). The same pattern was found for P concentrations among plots within blocks ($F = 2.9^{**}$) with a three fold higher variation (CV = 32 %) compared to C (CV = 11 %) and N (CV = 12 %).

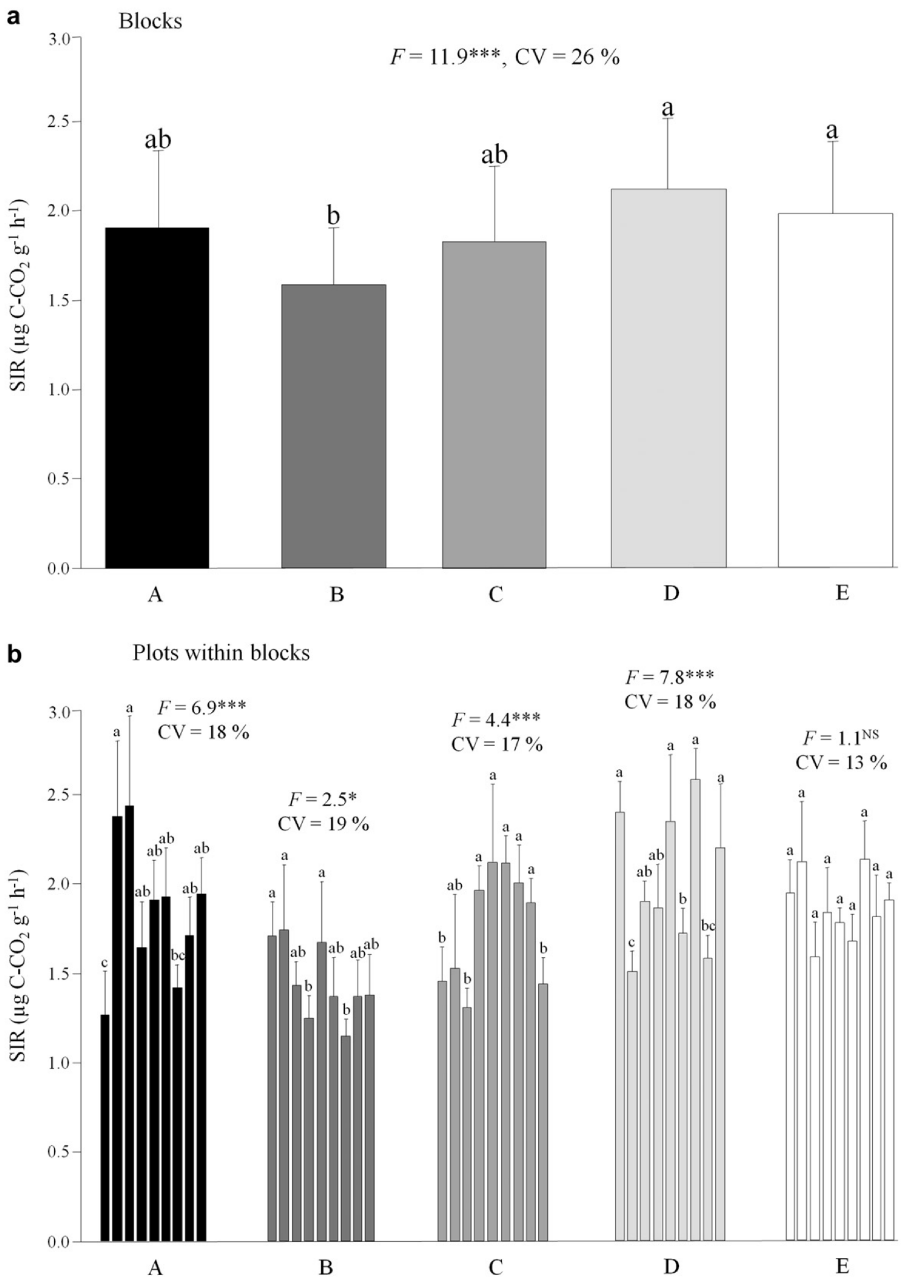

Figure 1 : SIR rates across the two scales examined in an undisturbed tropical rainforest of French Guiana (mean ± SD). (a) Blocks, (b) Plots within blocks. Different letters indicate significant differences between blocks or plots within blocks (P < 0.05, Tukey HSD tests).

The C:N ratio showed an absolute range between 23.0 and 42.7, the C:P ratio between 759 to 4846, and the N:P ratio between 23.8 to 140.1. Litter stoichiometry differed significantly among blocks and also among plots within blocks, except for the C:P ratio.

The proportions of WSC, hemicellulose, cellulose, and lignin, as well as the concentration of condensed tannins, all varied significantly among blocks and among plots

within blocks. The lowest and highest average lignin concentration was measured in block E and block B, respectively, and increased significantly with decreasing total C concentration (R^2 = 0.360***, Appendix 1). Block A showed the highest concentration of condensed tannins (2.9 %) that was significantly higher than for all other blocks (Table 2).

Table 2. Quality (total concentration) and quantity of the litter layer sampled from the five studied blocks.

Litter characteristics†	A	B	C	D	E	*F value*‡ (Block)	C.V§	*F value*‡ (Plots within Blocks)	C.V§
Litter elements									
Carbon (%DM)	45.2 ± 2.5^{a}	38.5 ± 3.3^{c}	42.1 ± 2.4^{b}	42.4 ± 2.7^{b}	42.6 ± 2.0^{b}	35.6***	17%	5.0***	11%
Nitrogen (%DM)	1.31 ± 0.10^{a}	1.06 ± 0.20^{b}	1.30 ± 0.08^{a}	1.30 ± 0.11^{a}	1.40 ± 0.20^{a}	26.5***	18%	4.0***	12%
Phosphorus (%DM)	0.022 ± 0.004^{a}	0.020 ± 0.004^{a}	0.020 ± 0.005^{a}	0.023 ± 0.004^{a}	0.023 ± 0.002^{a}	2.8*	36%	2.9**	32%
Litter stoichiometry									
C:N	34.5 ± 3.1^{a}	26.9 ± 3.2^{b}	32.4 ± 1.6^{ab}	32.6 ± 3.6^{ab}	30.4 ± 2.7^{b}	21.1***	12%	5.7***	7%
C:P	2055 ± 217^{ab}	1925 ± 360^{b}	2105 ± 561^{a}	1844 ± 318^{b}	1852 ± 208^{b}	3.2*	37%	1.3^{NS}	30%
N:P	59.5 ± 8.9^{a}	53 ± 8.3^{b}	65 ± 18.5^{a}	56.5 ± 9.0^{a}	60.9 ± 7.1^{a}	6.9***	34%	1.7**	25%
C forms									
WSC (%DM)	26.6 ± 1.9^{b}	24.6 ± 2.8^{c}	25.6 ± 2.3^{bc}	29.2 ± 3.3^{a}	29.5 ± 2.4^{a}	22.5***	15%	3.6***	10%
Hemicellulose (%DM)	11.5 ± 0.8^{a}	10.2 ± 0.8^{b}	11.1 ± 1.1^{a}	10.8 ± 1.0^{ab}	11.7 ± 1.1^{a}	10.4***	14%	3.0***	11%
Cellulose (%DM)	18.6 ± 1.9^{a}	14.9 ± 3.3^{b}	19 ± 1.3^{a}	16.5 ± 1.6^{b}	16.5 ± 0.9^{b}	24.9***	18%	3.8***	12%
Lignin (%DM)	43.3 ± 2.8^{b}	50.3 ± 4.1^{a}	44.2 ± 3.2^{b}	43.4 ± 2.1^{b}	42.3 ± 1.3^{b}	42.9***	10%	4.7***	6%
Tannin (%DM)	2.9 ± 0.6^{a}	1.5 ± 0.8^{b}	1.5 ± 0.6^{b}	1.3 ± 0.3^{b}	1.6 ± 0.4^{b}	34.7***	49%	3.1***	32%
Other litter traits									
Litter mass (g m^{-2})	417.3 ± 54.4^{b}	326.3 ± 83.5^{c}	528.4 ± 63.7^{a}	426.6 ± 94.0^{b}	606.7 ± 128.6^{a}	28.6***	38%	2.1**	27%
pH litter	4.8 ± 0.1^{ab}	4.8 ± 0.3^{ab}	4.6 ± 0.2^{b}	4.7 ± 0.2^{b}	4.9 ± 0.2^{a}	7.3***	7%	3.5***	5%

†Each value represents an average per block ± SD (n = 45 per block). Different letters indicate significant differences between block (P < 0.05, Tukey-HSD tests).
*‡For nested ANOVA, the F values and corresponding significance of the associated p-value are reported as follows: * (P < 0.05), ** (P < 0.01), and *** (P < 0.001) for the two scales (Blocks or Plots within blocks).*
§Coefficients of variation (CV) are given in percentage.

Litter mass per unit ground area also differed widely among blocks and among plots within block (Table 2). Block B showed the lowest (326.3 g m^{-2}) and block E the highest (606.7 g m^{-2}) amounts of litter per unit ground area. Finally, litter pH also differed among blocks and among plots within block, with highest values measured in block E and lowest values measured in blocks C and D (Table 2).

The first two axes from PCA on litter traits accounted for 49.9 % of the total normalized variance of the 10 litter variables (Fig. 2a). The first axis, explaining 33.4 % of the variance, was positively related to litter C, N, P and litter mass and

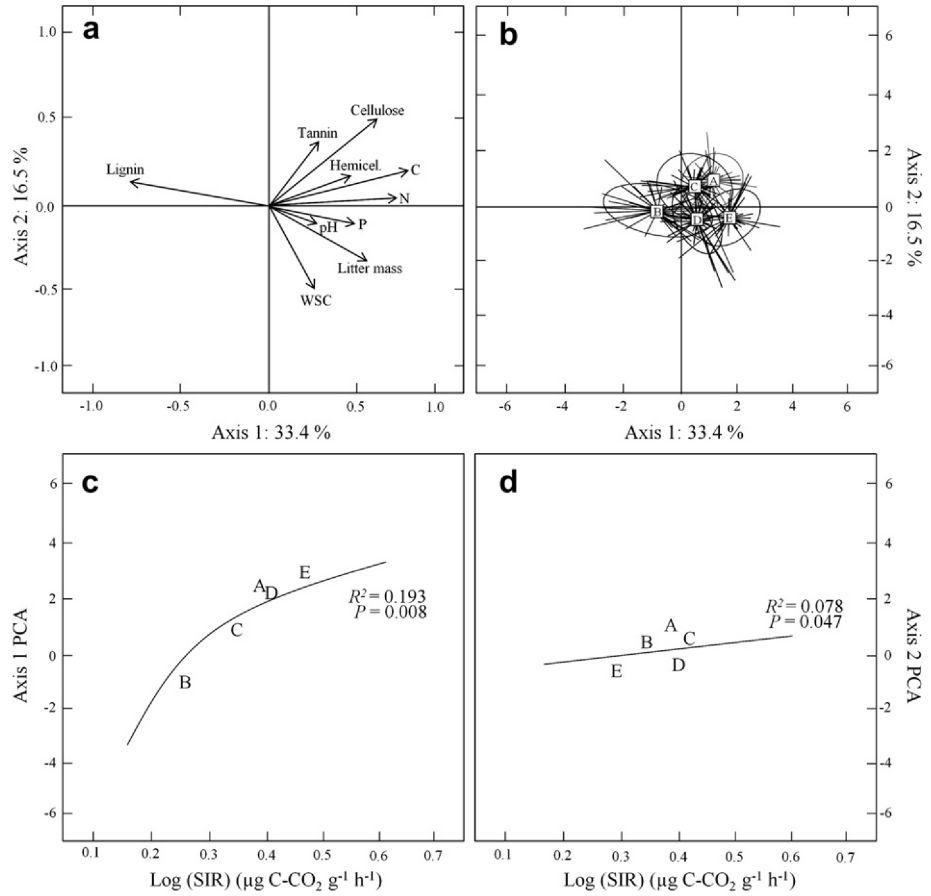

Figure 2 : Analysis of litter traits: (a, b) principal component analysis (PCA) using aggregated traits, and (c, d) the relationship between PCA axes and SIR rates. (a) Two orthogonal axes explain 33.4% and 16.5% of the variance. The end of the arrows indicates component loading. (b) For the intra-class analysis, the lines correspond to the distance between calculated barycenter and projection of the different samples per block. The circles represent the average projection area of samples from the barycenter for each block. (c, d) the regressions were computed between log-transformed SIR rates and PCA scores for the first two axes. Litter traits: concentrations of C, N, P, WSC, hemicellulose, cellulose, lignin, condensed tannin, litter mass (g m^{-2}) and pH.

negatively to lignin concentration. The second axis accounted for 16.5 % of the total variance and was related to carbon forms with positive contributions of tannin and cellulose concentrations, and a negative contribution of litter WSC concentration. Hence, two independent axes of specialization were identified. The intra-class analysis allowed the visualization of the relative position of the different blocks (Fig. 2b). Block B appeared to be somewhat detached from the other blocks and contributed negatively to the first axis. Blocks D and E conversely to blocks A and C showed a slight differentiation along the second axis.

3.3. Relationships between litter quality and soil SIR

SIR rates correlated with the first axis from PCA scores (Fig. 2c), and more weakly with the second axis (Fig. 2d). Linear mixed models also displayed significant relations between SIR rates and individual litter quality traits. SIR rates were positively influenced by the total litter P content and, to a lesser extent, by total litter N and C contents (Table 3). However, there was no relation between SIR and litter C:N, C:P or N:P. The variation in SIR was also influenced to some degree by the variation in litter C forms (Table 3). Lignin, WSC and hemicellulose contents respectively, displayed significant relations with SIR rates. However, SIR rates decreased with increasing litter lignin content, whereas they increased with increasing WSC and hemicellulose contents.

When fitting models with litter traits that individually significantly correlated with SIR, we could explain about 30% of the variation in SIR with total litter P, N and C contents, while the combination of total litter lignin, WSC and hemicellulose contents accounted for about 39% of the observed variation in SIR (Table 4). When litter C forms were combined with total C, N and P litter contents, the best fit explaining 50% of the variation in SIR rates was obtained (Table 4).

Table 3. Results of linear mixed model on SIR rates for the effects of scale (blocks and nested plots), litter element (C; N; P), stoichiometry (C:N; C:P; N;P), carbon forms (WSC; Hemicellulose; Cellulose; Lignin; Tannin) and other litter traits (pH; Litter mass).

Factor

Random effect			Estimates	Std. Err.	Wald $Z^{‡}$
Blocks			0.00124	0.000083	9.3***
Plots within blocks			0.00066	0.000044	5.5***
Residual			0.00487	0.000325	16.2***
Fixed effect	Num. d.f.†	Den. d.f.†	Effect	*F value*	*P value*
C	1	207	+	4.4	0.035
N	1	207	+	28.1	< 0.001
P	1	207	+	53.7	< 0.001
C:N	1	207		0.4	0.50
C:P	1	207		0.6	0.47
N:P	1	207		0.8	0.37
WSC	1	207	+	7.9	0.005
Hemicellulose	1	207	+	5.7	0.02
Cellulose	1	207		0.2	0.7
Lignin	1	207	-	44.3	< 0.001
Tannin	1	207		0.9	0.33
pH	1	207		0.9	0.34
Litter mass	1	207		0.01	0.92

†Num d.f., numerator degrees of freedom; Den d.f., denominator degrees of freedom.
*‡Wald statistic value for random effects significant (*** P < 0.001).*

Table 4. Best-fit linear mixed models of SIR rates as a function of significant litter quality traits (total content).

Model equation[a]	R^2	AIC
Litter nutrients and carbon content variables only $\log(SIR) = 0.64 + 0.30 \times \log(P) - 0.06 \times r{-}s(N) - 0.003 \times r{-}s(C)$	0.30	404
Carbon forms content variables only $\log(SIR) = 0.78 - 0.40 \times \log(lignin) + 0.06 \times \log(WSC) + 0.04 \times r{-}s(hemicellulose)$	0.39	433
Combined litter nutrients and carbon forms variables $\log(SIR) = 1.52 + 0.29 \times \log(P) - 0.39 \times \log(lignin) - 0.06 \times r{-}s(N) + 0.02 \times r{-}s(C) - 0.10 \times \log(WSC) + 0.003 \times r{-}s(hemicellulose)$	0.50	456

*†All regressions are significant at *P < 0.05.*

4. Discussion

4.1. Spatial variability of soil microbial respiration process and litter quality

We initially hypothesized that the high variation in leaf litter quality, typical for tree species-rich tropical forests, determines the spatial variability of microbial respiration process in the underlying soil to an important degree. We explored this hypothesis with a large nested sampling effort across a 2.5 ha area in an undisturbed forest of French Guiana. The 225 paired samples showed an impressive variation in chemistry of the standing litter layer and in soil SIR.

SIR rates ranged from 1.1 to 4.0 μg of C-CO_2 released per gram of soil per hour. These results compared well with previous measures of SIR in a different part of the same study site at Paracou ranging from 0.2 and 4.0 μg C-CO2 g^{-1} h^{-1} (N. Fromin, unpublished data). Kosugi *et al.* (2007) have recently shown that the variation of actual soil respiration increased from scales of 10 m and less to scales of 50 m. In line with this previous study, the CVs of SIR measured in our study increased with increasing scale from 17 % at the plots within blocks scale to 26 % at the blocks scale, confirming the intuitively expected increase in variation of microbial respiration process with a relatively small increase in scale. While it is generally accepted that spatial variation of soil respiration is primarily controlled by abiotic factors (Davidson *et al.,* 1998; Khomik *et al.,* 2006; Adachi *et al.,* 2009), it has been shown that soil respiration measured in situ at scales of 10 m and less does not co-vary with small differences in soil temperature or moisture (Epron *et al.,* 2006; Martin & Bolstad, 2009). These data clearly suggest that biotic factors related to plant presence and forest structure gain in importance as drivers of microbial respiration process at small spatial scales.

Litter quality collected from the ground was highly variable across the five blocks and also at the scale of the plots within blocks, but to a lesser degree (Table. 2). These results reflect the high variation in quality of freshly fallen leaf litter among co-occurring tree species in this highly diverse forest (Hättenschwiler *et al.,* 2008). Less variation in litter quality among plots within blocks than among blocks is in line with the expected greater divergence of tree species composition and the associated litter input at larger than at small spatial scales. However, the variation in litter quality among plots within blocks remains

substantial, because of the juxtaposition of litter originating from different tree species (locally 6 to 9 species at the scale of one square meter at our study site). The unique local characteristics of each litter mixture at a given time are further enhanced by variable litter fall dynamics leading to large differences in the distribution of the annual litter fall among tree species (Bréchet *et al.,* 2009).

4.2. Microbial respiration process in relation to litter quality

SIR rates correlated significantly with litter layer quality. Among the different quality traits, total P content in the litter layer was the single most important factor explaining the observed spatial variation. Higher SIR rates with increasing P availability might be expected in the studied extremely P-poor tropical forest. Recent studies have shown that the addition of P in P-limited tropical forest ecosystems increase the mineralization of dissolved organic matter derived from litter (Cleveland *et al.,* 2002; Cleveland *et al.,* 2006) as well as litter decomposition rates (Hobbie & Vitousek, 2000; Kaspari *et al.,* 2008). Higher litter N content was also positively correlated with soil SIR, but to a lesser extent than was observed for litter P content. This might indicate less N than P limitation in line with the commonly proposed shift from N to P limitation from high to low latitudes (Reich & Oleksyn, 2004; Vitousek *et al.,* 2010). This finding is in agreement with the study of Bréchet *et al.* (2009) who reported a strong relationship between actual soil respiration measured in situ and litterfall P and N in planted monocultures of sixteen tropical tree species in close vicinity to our study site.

In addition to litter layer nutrient contents, total litter C content also correlated positively with SIR rates. Increasing litter C content was associated with relatively low proportions of lignin, and thus, relatively high proportions of more easily accessible C compounds such as WSC and hemicellulose. Such proportionally higher availability of more labile carbon compounds providing easier access to limiting energy likely explain the positive effect of increasing litter C content on soil microbial respiration process that is in line with the proposed energy limitation of decomposer communities in our study system (Hättenschwiler *et al.,* 2010). Similarly, Cleveland *et al.* (2007) reported a rapid and large increase in soil CO_2 efflux in response to the addition of dissolved organic matter in a Costa Rican tropical forest. A higher relative availability of soluble, easily available C compounds

may additionally enable the access to limiting nutrients contained in more recalcitrant C compounds through priming (Kuzyakov *et al.,* 2000). Such interactions between carbon and nutrient cycles could be of paramount importance for the understanding of resource limitation of microbial-driven processes and ecosystem nutrient dynamics. These interactions are expressed at small spatial scales since the tight links observed between litter-soil couples, which strongly vary at small scales, show that litter control of microbial respiration process is a patchy phenomenon. Such small-scale control might have important implications for soil nutrient availability and related feedbacks on the plant community.

Contrary to our expectation of important litter stoichiometry effects, SIR was not related to litter stoichiometry. Substrate stoichiometry was described as a critical component for trophic relations in aquatic (Elser *et al.,* 2000; Sterner & Elser, 2002) as well as in terrestrial ecosystems (Cleveland & Liptzin, 2007). However in our study, the C:N:P ratio appeared less important than the absolute amounts of these elements, in particular of P. A possible explanation for the apparent lack of correlation between C:N:P stoichiometry and microbial respiration process might be the constantly changing litter stoichiometry during decomposition. The single harvest of the litter layer might not representatively reflect litter stoichiometry dynamics and how they influence the underlying soil. Moreover, the stoichiometry of bulk litter material might not accurately reflect the stoichiometry of some key compounds preferentially exploited by microorganisms. A third not mutually exclusive explanation is that stoichiometry might act rather through changes in microbial community composition and not necessarily through changes in their functioning. Future research should attempt to assess if and how microbial community composition depends on litter stoichiometry and whether or not microbial stoichiometry or community structure traces litter stoichiometry. The much larger variety and higher quantity of rather recalcitrant organic C forms in terrestrial compared to aquatic ecosystems may also prevent detecting clear effects of organic matter stoichiometry on microbial respiration process.

Finally, it is possible that soil microorganisms and associated processes might be more influenced by the quality and stoichiometry of soil parameters, although such parameters appeared to be strongly controlled by the quantity and quality of organic matter inputs. In our study, concentrations of C, N, and P in the soil correlated strongly with that of the litter layer. Accordingly, SIR rates did also significantly correlate with total soil C (R^2 =

0.47***), N (R^2 = 0.44***), and P (R^2 = 0.27***) concentrations. However, based on our soil data we detected only very weak correlations between soil stoichiometry and SIR (data not shown), in line to what we reported for litter stoichiometry. A general model including soil and litter characteristics explained 66% of the variability in SIR rates, with 42% attributed to soil parameters against 24% attributed to litter parameters (data not shown). This relatively strong litter contribution clearly suggests that soil microbial respiration process is not sufficiently well explained by soil parameters alone, but depends on characteristics of the litter layer as well. These data reinforce our conclusion that microbial respiration process in the soil beneath a spatially heterogeneous litter layer is influenced by variable litter C and nutrients to an important degree. A continuous litter input of a specific quality obviously determines soil carbon and nutrient concentrations to a large extent. This imprint of aboveground litter input in soil characteristics is well known at larger spatial scales at the forest stand level. For example, conifer tree stands are characterized by a distinct humus form and organic matter quality compared to broadleaved deciduous tree stands grown in the same climate resulting in clear differences of soil parameters (Kalbitz *et al.*, 2000). However, we showed here for the first time that such aboveground litter impacts on microbial respiration process can even be observed at very small spatial scales in biologically heterogeneous forests. These results suggest that soil microbial respiration process is tightly linked to plant leaf litter input that varies particularly strongly in the tree species rich tropical forest studied here.

4.3. Conclusions

A significant part of variability in soil microbial respiration process in the studied Amazonian rainforest was related to the quantity and quality of the litter layer produced by a highly diverse tree canopy. In general, variation in P content and C forms correlated best with variation in soil microbial respiration process, suggesting that soil microorganisms are co-limited by P and labile C providing rapid access to energy. These relationships are tight at small spatial scales underlining the intimate relation between specific litter quality input at the patch scale and soil functioning. Our study provides evidence for an important plant

control of spatial variability in soil microbial respiration process beyond the more obvious autotrophic pathway related to the root-mycorrhiza system.

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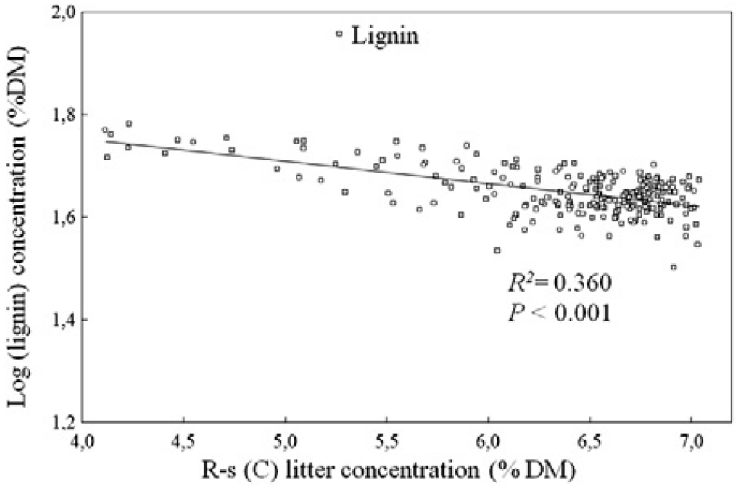

Appendix 1. Litter C concentration in % of dry matter (r-s transformation) as a function of lignin concentration (log transformation).

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Annexe C

Functional diversity of terrestrial microbial decomposers and their substrates

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ABSTRACT

The relationship between biodiversity and biogeochemical processes gained much interest in light of the rapidly decreasing biodiversity worldwide. In this paper we discuss the current status, challenges and prospects of functional concepts to plant litter diversity and microbial decomposer diversity. We also evaluate whether these concepts permit a better understanding of how biodiversity is linked to litter decomposition as a key ecosystem process influencing carbon and nutrient cycles. Based on a literature survey we show that plant litter and microbial diversity matters for decomposition, but that considering numbers of taxonomic units appears overall as little relevant and less useful than functional diversity. However, despite easily available functional litter traits and the well-established theoretical framework for functional litter diversity, the impact of functional litter diversity on decomposition is not yet well enough explored. Defining functional diversity of microorganisms remains one of the biggest challenges for functional approaches to microbial diversity. Recent developments in microarray and metagenomics technology offer promising possibilities in the assessment of the functional structure of microbial communities. This might allow significant progress in measuring functional microbial diversity and ultimately in our ability to predict consequences of biodiversity loss in the decomposer system for biogeochemical processes.

Keywords: Bacteria, Biogeochemical cycles, Decomposition, Dissimilarity, Ecosystem functioning, Functional diversity indices, Fungi, Leaf litter

1. Introduction

The fact that organisms not just passively live in a given environment but shape and change the environment around them is essential to understand biological evolution throughout Earth's history. For example, the Precambrian increase in atmospheric O_2 concentration, mainly as a result of oxygenic photosynthesis of cyanobacteria, changed the Earth's biogeochemistry fundamentally [1,2] and made the stunning evolution of oxygen dependent life possible (e.g. [3]). The physiology of organisms, the biogeochemical processes they influence, and the evolving diversity of organisms interact in many ways and are intricately linked. The functional relationship between biogeochemical processes and biodiversity, as one specific aspect of these interactions, gained considerable interest in light of the rapidly decreasing biodiversity worldwide [4,5] and its possible negative effects on ecosystem properties and functioning [6,7].

The efforts towards a better understanding of how ecosystem functioning and biodiversity are related focussed mostly on the impact of species richness on some key processes such as primary productivity [8-10] and decomposition [11-13]. While some early experimental studies provided evidence that increasing species richness of herbaceous plants is positively correlated with net primary productivity [8,14], following discussions and assessments highlighted the complexity of this relationship requiring careful interpretations of such correlative evidence from artificially composed communities [15-17]. Depending on which of the different mechanisms such as selection effects, facilitation or resource partitioning is at play, the interpretation of any correlation between plant species richness and productivity can be fundamentally different [15,17,18]. Moreover, the relation between species richness and productivity is temporally dynamic with both plant species richness and productivity changing with ongoing community development [19].

Obviously, mechanisms of biodiversity effects on ecosystem functioning cannot be understood by counting species, and the particular characteristics of organisms and their distribution in time and space need to be considered. For example, assembling herbaceous plants into just three functional types, i.e. legumes, forbs and grasses, allowed to account for a significant amount of variation in most biodiversity-ecosystem functioning experiments regardless of how many species were used (e.g. [10,18]). The fact that the presence of

nitrogen (N) fixing legumes was particularly important also provided an appealing mechanism for the observed positive biodiversity effects, that is increased N-availability at the community level, followed by higher productivity [18,20,21]. However, the presence of N-fixing plants is not a prerequisite for positive biodiversity effects on plant productivity [22,23]. Besides of grouping species into broadly and arbitrarily defined functional types, the well-established concept of functional traits [24-26] allows a finer grained characterization of functional diversity on the basis of objective and continuous variables [26,27]. While these traits and associated functions are coherently assembled for higher plants [28,29], such generally accepted lists of traits only start to emerge for other groups of organisms (e.g. [30]). The lack of a unified framework of functional traits outside the plant kingdom is particularly critical for hyper diverse communities organized in complex food webs such as soil organisms [31-34], for which a functional approach to diversity seems as one of few promising concepts to understand the role of biodiversity for ecosystem functioning.

With this paper we intend to explore the current status of functional approaches to the diversity of terrestrial microbial decomposers and their plant-derived substrates (plant leaf litter), and how functional diversity is linked to decomposition of organic matter as a key ecosystem process influencing the carbon and nutrient cycles. Unlike plant primary productivity that can be understood reasonably well by looking at plants as just one group of organisms within one trophic level, decomposition depends on many different groups of organisms across different trophic levels [32-33]. These different groups such as earthworms, saprotrophic fungi, or fungal feeding microarthropods, their functional roles and their importance in driving key soil processes are well recognized and intensively treated in the literature (e.g. [31,32,34-37]). However, functional diversity within groups of organisms and its impacts on decomposition is much less studied. Our assessment will be largely limited to terrestrial ecosystems despite the many similarities with aquatic decomposer systems [13].

2. Decomposition and the functional diversity of plant litter

Recycling of carbon (C) and nutrients during decomposition of dead organic matter is of key importance for ecosystem functioning. It determines the balance between the mineralization and sequestration of C, and soil nutrient availability to a great extent [38,39]. Up to 90% of the global terrestrial plant production can enter the pool of dead organic matter [40] with subsequent mineralization during decomposition. Rates of decomposition vary strongly depending on environmental conditions - with temperature and moisture as the most limiting factors to decomposer organisms - and also on the chemical and physical quality of the organic matter [41-44]. Litter quality traits that exhibit strong control over decomposition typically include litter N concentration, lignin:N ratio and C:N ratio [44-46], but may also be unrelated to N in non-temperate ecosystems such as in the Amazonian rainforest [47,48].

Related to climate and soil dependent plant traits and habitat-specific dominance of plant functional types, leaf litter quality varies widely among plant species across broad geographical scales [49,50]. However, there is also substantial variation among co-occurring plant species at the local scale of the plant community under identical environmental conditions ([51] Fig. 1). As a consequence, distinct litter types decompose together in

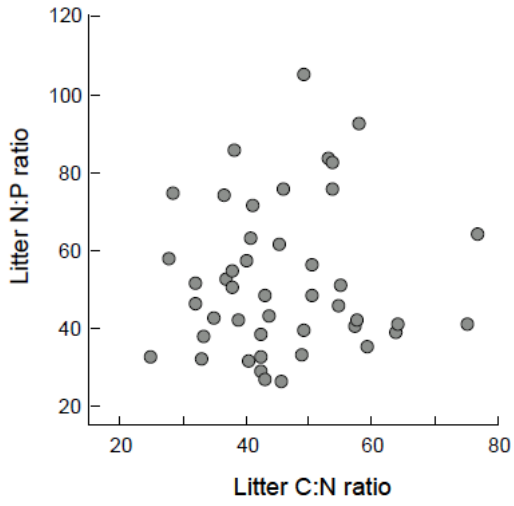

Figure 1: Leaf litter nitrogen : phosphorus ratio as a function of leaf litter carbon : nitrogen ratio from 45 Amazonian rainforest tree species co-occurring at the same site within a 0.98 ha forest area at Paracou, French Guiana. Each symbol represents the mean of a single species. Data from [51].

mixtures rather than in isolation from each other. Litter mixture decomposition has intensively been studied in recent years and the majority of these studies showed that litter mixture decomposition could not be predicted from the decomposition of single litter types included in these mixtures, with predominantly synergistic mixture effects (see reviews by [12,13,52]). These non-additive mixture effects typically show an idiosyncratic or no relationship with the number of litter species included in the mixtures (e.g. [11] Fig. 2). The seemingly unpredictable litter mixture effects on decomposition seriously hinders the development of a general mechanistic framework of litter diversity effects on decomposition that may allow the assessment of the impact of global change induced alterations of plant biodiversity on organic matter turnover and C sequestration.

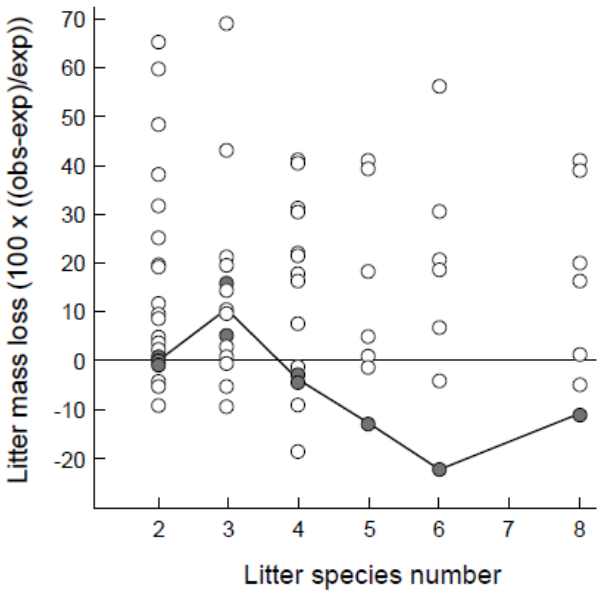

Figure 2: Litter mixture effect on litter mass loss measured after 300 days of decomposition in the field using litterbags as a function of litter species richness. The litter mixture effect is calculated as the observed litter mass loss (obs) of a mixture relative to the expected litter mass loss (exp) calculated from the corresponding single litter species treatments. Each symbol represents the mean (n = 4) of a specific mixture constituted from different species within functional groups (four sets: herbs from fertile cropping fields, grassland herbs, grasses and trees) or across functional groups (three additional sets). The filled circles connected with a line represent data points for grassland herbs as one of the total seven sets. Across all sets of species, the data show predominantly positive non-additive mixture effects (i.e. litter mass loss is greater than expected) and no relation with litter species number. Within the set of grassland herbs, mixture effects on litter mass loss show an idiosyncratic relationship with litter species number. Data modified and redrawn from [11].

A few years ago, Epps et al. [53] developed a theoretical framework that allows making abstraction of litter species identity and arbitrary diversity measures such as taxonomic richness, by considering functional traits represented by the different litter types. These functional traits were defined on the basis of commonly used chemical parameters of litter quality characterization and were used to define a multivariate chemical diversity

index as a weighted mean of compositional dissimilarity of litter mixtures [53]. Using published data, Epps et al. [53] showed that (1) there is considerable functional diversity within levels of litter species numbers, (2) the relationship between functional diversity and species richness varies among different plant communities, and (3) relationships between functional diversity and species richness can be negative, positive or idiosyncratic for the same set of litter types, but with three different series of additive mixtures (see Fig. 4 in [53]). According to the reasonable assumption that resource heterogeneity of litter mixtures drives the activity of decomposers and ultimately decomposition, they concluded that litter diversity – decomposition studies based on species richness as diversity measure almost necessarily result in idiosyncratic relationships, and that the proposed chemical diversity index based on Rao's quadratic entropy better reflects the functionally relevant diversity of litter mixtures [53].

In light of the rapidly developing body of literature on the pertinence and relevance of different measures of functional diversity [27,54-56], the considerations by Epps et al. [53] were not particularly novel in general terms, but these authors theoretically applied the concept of functional diversity for the first time to litter mixtures. The application of functional diversity to non-living "remains of a plant community" may be somewhat unconventional. However, the functional traits for the characterization of plant leaf litter are largely the same as those used for green plant foliage [57] and are traditionally used as predictors for decomposition [50]. It is thus surprising that the convincing ideas and suggestions by Epps et al. [53] have only rarely been tested experimentally.

The first study applying an explicit approach of functional diversity for litter mixture decomposition used litter from four alpine herbaceous species [58,59]. These authors determined nine mostly C-related chemical litter traits, and calculated the Shannon diversity index for all litter treatments including all possible mixtures of the four litter types. The Shannon diversity index accounts for both the presence and abundance of all measured litter compounds, providing a chemical diversity index for all single species and multi-species litter treatments. Soil respiration and net N mineralization measured in microcosms with natural soil amended with the different litter treatments showed no correlation with litter species number [58]. In contrast, soil respiration increased and net N mineralization decreased with increasing chemical diversity, providing clear evidence that functional

diversity based on chemical traits rather than species numbers affects decomposition in this study system [58]. Working in a different ecosystem of a nutrient-poor neotropical lowland rainforest, Hättenschwiler and Bracht Jørgensen [60] measured decomposition of four litter species that varied distinctly in their C : N and N : P ratios in a field experiment. Creating all possible combinations of these litter types, they tested the hypothesis that litter mixtures decompose faster with an increasingly heterogeneous C : nutrient stoichiometry because decomposers would exploit stoichiometrically diverse litter mixtures more efficiently. Stoichiometric diversity was expressed with a "dissimilarity index" using the functional attribute diversity (FAD2) introduced by Walker et al. [61]. In short, the FAD2 places litter mixtures composed of stoichiometrically different litter types at higher scores than litter mixtures composed of stoichiometrically similar litter types. In line with their hypothesis, decomposition proceeded faster with increasing stoichiometric dissimilarity of litter mixtures, but was not affected by litter species richness (Fig. 3). However, the positive relationship between decomposition and stoichiometric dissimilarity of litter mixtures was only found in the presence of soil macrofauna but not in their absence. Moreover, litter C quality (mostly the abundance of labile C compounds) had an overall stronger control over decomposition than stoichiometric dissimilarity. In a different study, Barantal et al. [62] tested the hypothesis that functional diversity correlates with litter mixture decomposition using an extensive set of 28 different litter mixtures created from a pool of litter collected from 16 Amazonian tree species. On the basis of eight chemical litter traits including N, P, and different C compounds, they used three distinct indices to describe functional diversity of litter mixtures in order to account for different aspects of functional diversity. Functional richness, functional divergence, and functional equitability were expressed with the FD index [63], Rao's quadratic entropy [53,64], and the Shannon index [e.g. 58], respectively. The frequent and at times strong non-additive litter mixture effects on decomposition observed by Barantal et al. [62], however, were not correlated to either of the different functional diversity indices. Rather they found that the presence of particular species was determining non-additive responses of litter mixture decomposition.

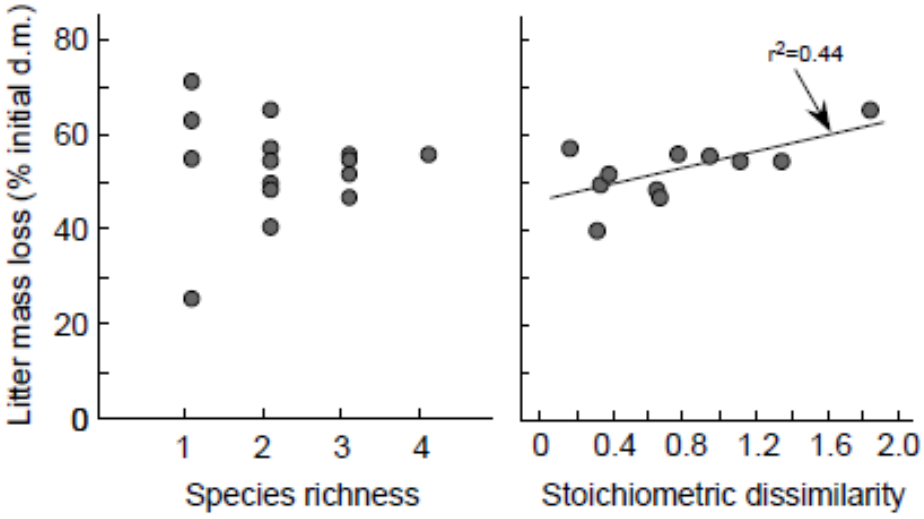

Figure 3: Litter mass loss (in % of total initial dry mass (d.m.)) after 204 days of decomposition in the tropical rainforest of Paracou, French Guiana as a function of litter species number (left panel) or as a function of stoichiometric dissimilarity (right panel). Soil macrofauna had access to the field microcosms. In the left panel, each symbol represents the mean (n = 4) of four single species treatments, six 2-species mixtures, four 3-species mixtures and one 4-species mixture. In the right panel, each symbol represents the mean (n = 4) of the 11 different mixtures along the dissimilarity gradient. Data modified and redrawn from [60].

The very few studies that experimentally explored how functional diversity of litter mixtures is related to the decomposition of these mixtures provided conflicting results. Some of these contrasts may be related to different study systems with different environmental constraints and/or to the use of different chemical litter traits for the calculation of functional diversity indices. Because this latter point is critical Barantal et al. [62] calculated functional diversity from several possible combinations of the eight measured traits with essentially no difference among the correlations between mixture effects and functional litter diversity. However, it is still possible that some key traits have not been measured and that consequently the functional diversity indices may not reflect the critical differences among distinct litter mixtures well enough. The suggestion to characterize litter quality by means of reflectance spectroscopy such as DRIFTS (diffuse reflectance infrared Fourier transform spectroscopy) or NIRS (near infrared spectroscopy) [53] which provide an integrated quality measure, thus seems worth to be explored in more detail. The evaluation whether functional litter diversity may or may not predict mixture effects on decomposition is currently data

limited and would benefit greatly from a wider application in new experiments to come or in already existing data sets.

3. Functional diversity of microbial decomposers

Soil bacteria and soil fungi are highly diverse groups of organisms with recent estimates based on high throughput DNA sequencing techniques ranging roughly between 2'000 and 20'000 Operational Taxonomic Units (OTUs) per gram of soil for bacteria [65,66] and between 1'000 and 2'000 OTUs per gram of soil for fungi [67,68]. The great diversity of microorganisms is paradoxically also the major obstacle in the understanding of the functional role of this diversity. It seems impossible to track and functionally describe each microbial taxon of a given community, and linking taxon identity to function is a major challenge in microbial ecology [69]. Consequently, microbial communities are currently treated as a "black box" in ecosystem models considering microbial diversity as unimportant which may be problematic for the assessment of how ecosystem processes are impacted by biodiversity change (e.g. [70]). Indeed, soil microorganisms are by far the major drivers of soil carbon and energy flow and nutrient transformations and mineralization. Whether or not these key ecosystem processes depend on microbial diversity and to what extent microbial diversity is sensitive to environmental change is presently not well understood.

A theoretical model predicted a positive effect of microbial diversity on decomposition resulting from more intense microbial exploitation of organic matter through functional niche complementarity [71]. This theoretical prediction is supported by the classical culture-based laboratory work that established the specialization of different fungal species for different carbon forms suggesting resource partitioning (e.g. [72,73]). Further, successional dynamics of microbial communities with ongoing litter decomposition demonstrated that microbial communities shift with the progressive change in resource availability [38,74,75]. A major limitation of this early work was the artificial conditions of laboratory cultures excluding the majority of species that would naturally occur but that are not culturable [76]. Recent studies using soil from a temperate forest [77] or decomposed litter from a boreal forest [78] very elegantly circumvented the major methodological

shortcomings of earlier studies. Adding either different C sources [77] or different N compounds [78] together with a nucleotide-analogue tag to the naturally established microbial communities, followed by quantitative polymerase chain reaction (qPCR) and sequencing of fungal communities, these authors were able to determine the structure and richness of active fungal communities under close to natural conditions. Both studies clearly showed resource preferences among fungal taxa resulting in shifts in community structure and richness as a function of different resources. The data from these studies are perhaps the currently most convincing experimental evidence for resource partitioning among soil microbial taxa under natural conditions. They further imply functional diversity of microbial communities and suggest that decreasing fungal diversity reduces the efficiency of the use of heterogeneous resources and thus the rate of decomposition.

For obvious reasons, direct manipulative tests of the effects of changing microbial diversity on ecosystem processes are difficult to perform and rely on either artificially reduced community diversity (e.g. dilution, fumigation) or on the synthetic composition of artificial communities from a few isolated and culturable taxa (e.g. [79-86]). These approaches are biased towards "resistant" or culturable taxa, which are unlikely to represent well natural microbial communities, as a major difficulty for data interpretation in a natural context as was already mentioned above. Despite this limitation, we will have a closer look at some of these studies and what they tell us about how process rates may depend on microbial diversity. We focus on two of these studies that allow the evaluation of mechanisms of diversity effects. This will permit to take the discussion a step further beyond taxonomic or genetic diversity towards functional diversity. The study by Tiunov and Scheu [85] nicely showed some of the operating mechanisms for diversity effects and the importance of functional aspects. They inoculated sterilized forest soil or powdered cellulose with five common species of saprotrophic fungi in all possible combinations from monocultures to all five species. Two species were fast growing cellulolytic species, one was also cellulolytic but relatively slowly growing, and two species were from the zygomycetes or the so-called "sugar fungi" that are not able to degrade cellulose. On both substrates, decomposition increased with increasing numbers of fungal species (Fig. 4). Selection effects, i.e. the increasing probability of the presence of at least one of the two fast-growing species in more species-rich communities, and complementarity effects, both contributed to higher

process rates of more species-rich communities [85]. The use of two substrates, the complex multi-resource forest soil, and the simple single-resource cellulose allowed evaluating the "complementarity component" of the diversity effect in more detail. Counter expectation, the complementarity effect on forest soil was weaker than on cellulose resulting in an overall weaker positive relationship between community respiration and species richness on forest soil compared to cellulose (Fig. 4). This result is interesting in that it shows that facilitation among fungal species apparently contributed more to the overall complementarity

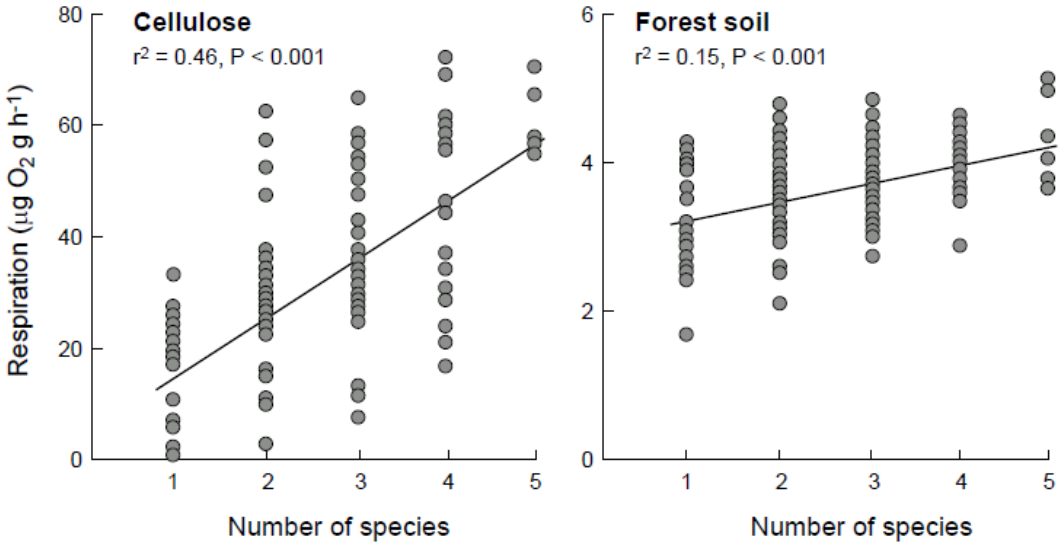

Figure 4: Community respiration of fungi as a function of fungal species richness on cellulose as the sole substrate (left panel) or on forest soil as a complex substrate (right panel). Data modified and redrawn from [85].

effect than resource partitioning, a mechanism that should not operate on cellulose as the single uniform substrate. In particular, the presence of cellulolytic species facilitated the growth and activity of sugar fungi probably through the production of intermediate products during enzymatic degradation of cellulose. Tiunov and Scheu [85] further hypothesized that the sugar fungi may increase the enzymatic activity of the cellulolytic species through the uptake of inhibitory sugars. The facilitative interactions between these two "functional groups" of fungi, however, were not sufficient for the observed complementarity in the treatments with cellulose as the sole C substrate. The combination of any of the three cellulolytic species alone increased community respiration additively as if

the three species grew on distinct substrates with complete resource partitioning. This surprising result is in line with a similar study that also used cellulose as the sole C source, but manipulated bacterial species richness to test diversity effects on cellulose decomposition [84]. In this study, microcosms were composed of bacterial communities of one, two, four, and eight species, randomly chosen from a pool of 10 cellulolytic bacteria, and maintained under constant environmental conditions. Despite the deliberate selection of "functionally redundant" species growing on the same resource, species richness facilitated species coexistence, increased the number of individuals, and increased cellulose decomposition in treatments with more than two species [84]. These results suggest again facilitation among *a priori* functionally similar species as the main mechanism of diversity effects. Such facilitation may arise due to small differences in the production of the required cocktail of cellulose degrading enzymes among species, or differential use of intermediate products, enzymes, secondary metabolites and metabolic waste products.

These two studies showed that microbial species from the same functional group of cellulose degraders growing on cellulose as the uniform substrate still exhibit "enough" functional dissimilarity that their combined presence in higher diverse communities results in higher process rates and in the case of the study by Wohl et al. [84] also in higher individual densities. Collectively, it seems that there exist ample possibilities for synergistic interactions among microbes through facilitation and resource partitioning even without environmental heterogeneity or strongly divergent resources. However, process rates are ultimately limited and the two studies that used wider species richness gradients beyond 10 species showed that process rates may saturate at relatively low [83] or higher levels [86] of species richness. A functional classification of microbial decomposers based on functional traits as continuous variables similar to the well-established trait framework for plants would greatly advance the possibilities to test and better understand the relationship between decomposition and microbial diversity. A functional approach to microbial diversity may also improve the predictability of the so far only generally and quite loosely described link between microbial community composition and ecosystem process rates (see [70] for review). In fact, changes in the composition and structure of microbial communities can be a rather poor indicator for associated changes in microbial-driven processes [87,88]. In

particular, communities that are more similar regarding their taxonomic composition may not necessarily be more similar regarding their functional capabilities [87].

Some of the big questions surrounding functional approaches to microbial diversity are how to define functional diversity of microbes, and what and how to measure functional traits of microbes. In the following we will list some possible ways to deal with these questions that may allow working towards the ambitious goal of a functional classification of microbes. A useful, but rather coarse-grained approach is the definition of functional groups such as the contrasting groups of sugar fungi and cellulolytic fungi discussed above [85]. For example, in a recent paper, Miki et al. [89] defined microbial functional groups based on the competitiveness on specific substrates, and used these functional groups to incorporate the role of microbial diversity in a plant- soil microbe feedback model. Similarly, McGuire et al. [78] characterized the functional diversity of fungal communities using the response of individual taxa to specific substrates. Whereas these two previous studies characterized microbial functional diversity at the level of individual culturable strains / isolates, Moorhead & Sinsabaugh [90] proposed to define the functional role of microbial communities on the basis of broad chemical traits of plant litter. They suggested to distinguish just three guilds of microbial decomposers that use broadly different pools of organic matter: a guild of 'opportunist microorganisms' with high affinities for soluble substrates and high growth rates, a guild of 'decomposer specialists' with a high affinity for holocellulose and intermediate growth rates, and finally, a guild of 'miners' that is specialized for degrading lignin and grows slowly. This is a strongly simplified view of microbial functional diversity that, however, would permit the incorporation of at least some level of microbial diversity into decomposition models.

Some more detail in the assessment of functional diversity of microbial communities is possible with the use of the "community level physiological profiles (CLPP)" [91]. These authors proposed to use the catabolic potential of microbial communities for their functional characterization. The catabolic potential describes the range, the diversity, and the intensity of resource use of microbial communities when offered a wide range of different substrates. The catabolic potential characterizes the "functional ability" of entire microbial communities. Such functional characterization of the whole community was also recently used to assess rates of denitrification as a function of various carbon sources [92]. These authors used 16

different species of denitrifying bacteria growing alone or in combination on various carbon sources. Interestingly, they demonstrated that denitrification of a given assembled community could be calculated from the individual species performance. Hence, the performance of individual species constituting a specific denitrifier community allows predicting the "community niche". However, while CLPPs or community niche approaches are useful to characterize and compare the functioning of entire communities under for example distinct environmental conditions, they don't really allow describing the functional diversity within communities. Moreover, CLPPs also failed to correlate with enzyme activity during decomposition [93] or with carbon mineralization (Fromin et al. *unpublished*) in other studies, suggesting that some key activities or processes are not always well predicted by CLPPs.

Molecular tools are probably among the most promising approaches to establish a connection between genetic identity and function of microbes, and the ecosystem processes they drive. Conventional molecular techniques targeting genes implied in specific functions have been used extensively for the characterization of microbial functional groups, but only rarely as a measure of functional diversity of microbial communities [94]. A particular difficulty in the context of how microbial diversity relates to decomposition is the fact that decomposition is a highly complex process involving many different enzymes and thus a multitude of genes coding for the expression of these enzymes. The recent developments in microarray and metagenomics technology offered new opportunities to assess the functional structure of microbial communities. For instance, the GeoChip [95] that contains > 24 000 probes and covers 150 gene families involved in biogeochemical C, N and P cycling is highly promising for studying the relationship between functional gene structure of the microbial community and ecosystem processes such as decomposition. For example, Zhang et al. [96] showed that the diversity of functional genes expressed under changing land cover tended to correlate with increasing amounts of soil organic carbon during decomposition. Finally, metatranscriptomic and pyrosequencing based approaches also present highly promising tools for the assessment of microbial functional diversity, but these applications are still in its infancy [97,98].

Assessing functional diversity for the taxonomically very rich microbial decomposer communities is obviously very challenging. There are a number of promising new

techniques and tools being developed that if applied in concert might allow this field of research to advance rapidly. At present, however, there is no single approach that would permit to describe the relevant functional microbial diversity for decomposition. Decomposition as such might be a too broad process to be described with a simple functional diversity measure of microorganisms. Instead, it might be more promising to focus on simpler processes driven by microbes, such as cellulose degradation or nitrification.

4. Conclusions

Our brief overview showed that plant litter and microbial diversity matters for decomposition of plant litter as a key ecosystem process influencing carbon and nutrient cycles. Considering numbers of taxonomic units appears overall as little helpful for the understanding and quantification of how decomposition depends on biodiversity. A functional classification of biodiversity based on functionally relevant traits of organisms seems a more promising approach. These functional traits are generally well defined and easy to measure for plant litter, but currently much more difficult to establish for microorganisms. Despite easy access to plant litter traits, studies evaluating litter mixture decomposition that used explicit functional diversity approaches are very few. Some of these studies clearly showed that trait-based functional diversity predict litter diversity effects on decomposition better than litter species richness. It would be highly interesting to re-analyze the multitude of litter diversity experiments using a unified functional diversity approach, possibly with the application of alternative techniques such as DRIFTS or NIRS to characterize litter quality in an integrative way. Perhaps the biggest challenge for functional approaches to microbial diversity is how to define functional diversity of microbes, and what and how to measure functional traits of microbes. There are a number of promising new techniques and tools being developed such as the GeoChip that might allow significant progress in the near future.

Interactions across the trophic levels of plant-derived substrates and microbial decomposers were only implicitly treated in our analysis and would merit a closer examination. Such interactions may modify the impact of functional diversity within trophic

levels on process rates [13, 99, 100]. Even if this is adding further complexity to the assessment of how biodiversity drives ecosystem processes, the incorporation of food web complexity is ultimately indispensable for a mechanistic understanding of biodiversity effects on ecosystem functioning [13, 99, 100].

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