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Investigating diversity dependence of tropical forest litter decomposition: experiments and observations from Central Africa

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Abstract

Questions: Mixed litter may decompose at different rates to single-species litter, leading to differences in ecosystem functioning and decomposition. Studies of the effects of different litter species and combinations are rare in tropical forests and absent from African forests. Therefore we investigated: (1) Are there differences in litter decomposition in two forest types differing in tree diversity; and (2) is litter decomposition diversity-dependent?

Location: Old-growth moist evergreen tropical forest Dja Faunal Reserve, southeast Cameroon.

Methods: We calculate decomposition rates (leaf litter fall/leaf litter standing crop) along a tree diversity gradient in two forest types (naturally occurring low-diversity monodominant and adjacent higher-diversity mixed forest). Both forests experience the same climate on the same soil type; the former is dominated by a single species, *Gilbertiodendron dewevrei* (De Wild.) J. Léonard, probably due to lack of a long-term disturbance and has similar edaphic factors. Decomposition experiments were conducted in both forest types using single and mixed species litter bags of standard high-quality (bay leaves; *Laurus nobilis* L.) and low-quality (*G. dewevrei*) litter over 9 months.

Results: The estimated decomposition rate in mixed forest was four times faster than in monodominant forest, and not significantly correlated with local quadrat-scale tree species diversity. The litter bag experiment showed that decomposition of high-quality leaves was faster than low-quality leaves (*k* values: 2.0 yr^{-1} vs 0.6 yr^{-1}). Decay rates for each single species litter type were not significantly different in both forest types. However, *G. dewevrei* litter in mixed bags decomposed faster than in single-species bags in mixed forest, suggesting an impact of litter mixing on decomposition. In addition, bay litter in mixed bags decomposed faster in mixed than in monodominant forests across the three study sites.

Conclusion: The observed difference in litter decomposition rate between low-diversity monodominant and adjacent high-diversity forest is more likely due to dominance of low-quality *G. dewevrei* litter, rather than low-diversity of the litter itself.

Introduction

Litter decomposition is a major pathway for nutrient cycling, by which carbon (C), nitrogen (N), phosphorus and other elements move from plants to the soil, back to plants and to the atmosphere (Coûteaux et al. 1995). Understanding the influence of factors such as the physical and chemical properties of plant litter, i.e. 'litter quality' (Aerts 1997; Bernhard-Reversat & Schwartz 1997; Bernhard-Reversat 1998), soil fauna (Heneghan et al. 1999)

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and environmental variables (Meentemeyer 1984), on litter decomposition has been the focus of many decomposition studies. The main factors controlling decomposition rates in different ecosystems in different environments may vary. While litter quality and climate are considered to be the more important determinants in controlling decomposition rates in temperate ecosystems (Meentemeyer 1984), biotic factors (i.e. the decomposer community) appear to have a greater impact on regulation of decomposition in tropical ecosystems (Lavelle 1993). The contribution of soil fauna may vary among vegetation types (e.g. lowland and montane forests; González & Seastadt 2001) as may litter quality and species composition (Chapman et al. 1988; Silver & Miya 2001).

The importance of litter diversity in determining decomposition rates has been assessed in 30 studies (Hättenschwiler et al. 2005). The potential mechanisms that might drive such litter mixing or diversity effects on decomposition include nutrient transfer by fungi among leaf litter from different species, microbial inhibition or stimulation by specific litter compounds, and improved microenvironmental conditions for soil fauna (for more details see Hättenschwiler et al. 2005). However, most previous studies that considered mixtures of different litter species involved temperate ecosystems, with only one study from the tropics. An experiment in Panama (Scherer-Lorenzen et al. 2007) using six native tree species, with mixtures containing one, three or six species in a total of 24 experimental plots, found that number of species used did not change the decomposition pattern of the entire litter mixtures. However, the decomposition rate of individual species could be affected, depending on the diversity of the litter mixture (i.e. species-specific responses to mixing litter).

Here, we focus on a specific type of African tropical forest, which provides a unique natural experiment to test litter mixing and litter diversity decomposition hypotheses, because high-diversity forests co-occur with areas of natural, old-growth, low-diversity forest (see Peh et al. 2011a). Furthermore, these diversity differences are not caused by differences in climate or known soil physical or chemical characteristics (Hart et al. 1989; Conway 1992; Peh et al. 2011b). The low-diversity forests are generally considered to have had little disturbance, perhaps for thousands of years (Connell & Lowman 1989; Hart et al. 1989) but do not appear to be in a retrogressive phase in the prolonged absence of disturbance (i.e.,decline sensu Vitousek & Farrington 1997; Wardle et al. 2008), because the difference in nutrient availability between low-diversity and the adjacent high-diversity forests is not significant (Hart et al. 1989; Peh et al. 2011b) and there is no evidence that tree biomass in the low-diversity forests is declining (see Chave et al. 2008; Lewis et al. 2009).

An understanding of litter diversity effects on decomposition rates in this system may be of importance for several reasons. First, there is much debate about diversity–ecosystem function relationships. Studies have shown that the effect of litter diversity on decomposition rates could be positive (e.g. Hector et al. 2000), negative (e.g. Madritch & Cardinale 2007) or neutral (e.g. Blair et al. 1990) but few investigations have been undertaken in the tropics. Second, there are few data on decomposition of litter mixtures. This system provides a unique opportunity to manipulate the diversity of the environment as well as diversity of the litter, to test for the environment–diversity functional interactions. Comparisons of decomposition dynamics between the monodominant and mixed species tropical forests allow study of effects of differing diversity under the same climate condition *in situ*. Finally, in the face of rapid loss of biodiversity (Bradshaw et al. 2009), it is essential to know how lower plant diversity might affect decomposition to better understand how key processes in tropical ecosystems might change if plant species richness declines. Furthermore, there is no previous study on the effects of litter mixtures in a tropical lowland forest setting, nor any study comparing decomposition processes of litter mixtures between monodominant and mixed forests in the tropics.

The present study is in two parts; first we quantify the amounts of leaf litter fall and ground litter of the monodominant and mixed forest systems to estimate decomposition rates; second, we conduct a factorial experiment using leaf litter of a two-species mixture (*Gilbertiodendron dewevrei* and *Laurus nobilis*) for comparison of decomposition rates with single-species litters (each of the two component species of the mixed litter) with all three combinations in both monodominant and mixed forest areas. If the decomposition rates are affected by litter composition (i.e. mixtures of litter), we expect a change in the decay of each component species in the mixture when compared to decomposition rates on the basis of a single species.

The litter bag experiment involved two treatments as it was conducted in both low-diversity monodominant forest and high-diversity mixed forest, to examine the effects of litter diversity on decomposition dynamics under prevailing conditions in the two forest types. The experiment also involves two levels in which we examine the responses of individual species within the litter mixture to facilitate comparison between high-quality litter (*L. nobilis*) and low-quality litter (*G. dewevrei*) species responses, where roles may differ in the different forest types. We also consider the role of tree species diversity through the effects of forest floor litter diversity on decomposition processes and the temporal pattern of the mixed litter effects to assess potentially complex decomposition processes in these tropical forests.

We addressed the following questions: (1) Do natural decomposition rates differ between two forest types differ-

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ing in species richness and community composition, as well as litter quality, and does this correlate with tree diversity? (2) What is the proportion of litter produced by *G. dewevrei* on the forest floor of monodominant *G. dewevrei* forest and does this litter fall abundance correlate with tree species diversity within monodominant forest? (3) Does tree species diversity affect estimated decomposition rates in the two forest types and those derived from litter bag experiments? (4) Do the two litter species of contrasting initial quality affect each other's decomposition rate when they are mixed? and (5) Do each of these different quality litters and their mixtures show similar patterns of decomposition over time in the two forest types?

Methods

Our study area was at the Dja faunal reserve (2°49′–3°23′N, 12°25′–13°35′E) in southeast Cameroon (Fig. 1). The reserve consists of continuous lowland moist forest on a plateau 500–700 m a.s.l. From 1979 to 2008, the recorded annual precipitation at the reserve ranged from 745 to 3275 mm (Peh et al. 2011b; mean annual precipitation was 1512 mm); maximum average monthly temperature was 25.8 °C, and minimum temperature was 23.6 °C (Peh et al. 2011b). The reserve experiences two wet seasons (May and Oct) and two short dry seasons (Dec–Feb and Jul –Aug) each year (Peh et al. 2011b).

We based our work around three independent, non-contiguous patches of monodominant forest and adjacent mixed forest within the reserve, and our study took place between Apri 2007 and Mar 2008. All three sites were more than 4 km from other sites. At each site we established one 100 m × 100 m plot within monodominant forest and another plot of the same size within the adjacent mixed species forest. The two plots within each site were <850 m apart. Each plot was located at a random position within each forest type by following a random compass bearing for a random number of metres to mark the location of the start point of the plot; orientation was then N–S. Each plot was divided into 25 quadrats (20 m × 20 m). We identified all tree species with stems >10 cm in diameter at breast height (DBH; 1.3 m or above all buttresses) in all quadrats and calculated their Simpson's tree diversity index. In total, we had six plots consisting of three pairs of monodominant and mixed species forest plots.

Soils in the plots of the two forest types are acidic weathered, clayey Ferrosols (also known as Oxisols; Peh et al. 2011b). Physical and chemical soil properties – soil bulk density, pH, particle size, C and N content, C/N ratio, concentrations of labile, inorganic and total (NaOH extractable) phosphorus and other trace elements such as aluminium (Al), boron (B), barium (Ba), calcium (Ca), cobalt (Co), chromium (Cr), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), molybdenum (Mo), sodium (Na), nickel (Ni), selenium (Se), silicon (Si), strontium (Sr), titanium (Ti), vanadium (V) and zinc (Zn) – along a depth gradient (0–2 m) were not significantly different between the monodominant and mixed forest plots (for description of soil analyses, see Peh et al. 2011b). Information on these forest plots is briefly summarized in Table 1.

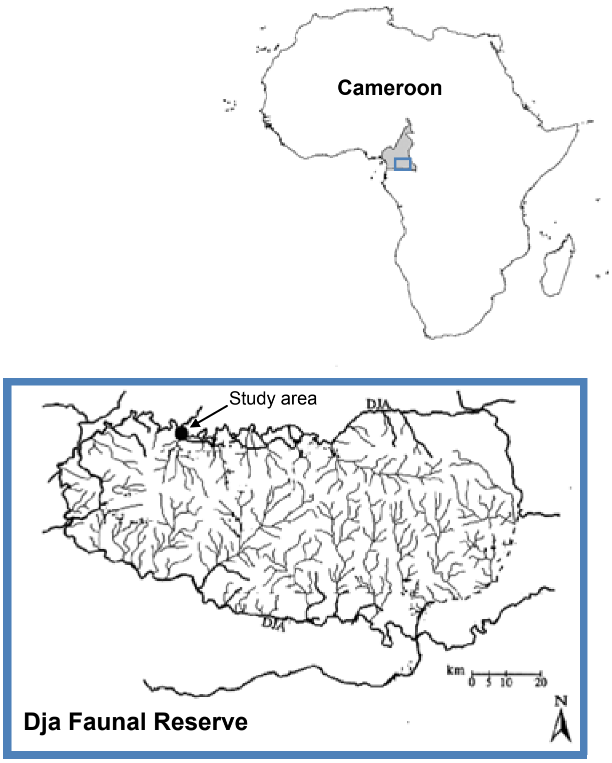

Fig. 1. Map of study location at the Dja Faunal Reserve in Cameroon.

Litter fall measurements

We collected leaf litter fall by placing three litter traps (0.5 m × 0.5 m, 1-mm mesh) in each of ten randomly selected quadrats in each of six plots (i.e. 30 traps per plot and 180 traps in total). The traps were randomly placed at least 5 m from the perimeter of the quadrats to minimize the influence of the adjacent quadrats (i.e. edge effect; Wardle & Zackrisson 2005). Fortnightly, we collected the contents of the traps for a period of 1 yr (Apri 2007–Mar 2008), dried the litter to constant dry mass, and weighed it to obtain an annual dry litter fall mass from each trap. The amount of *G. dewevrei* leaf litter fall derived from the traps in the monodominant forests was used to determine the proportions of *G. dewevrei* litter in leaf litter fall at a small-scale within the monodominant forest. Among the quadrats that had litter fall traps, we randomly selected three quadrats from each plot where we also measured leaf

Table 1. Summary of information on forest plots (1 ha) where litter decomposition observations and experiments were conducted from Apri 2007 to Mar 2008 including plot code, number of tree species, Fisher's alpha index; dominance of *Gilbertiodendron dewevrei*; total basal area and top soil (0–30 cm) parameters such as pH; carbon (C) and nitrogen (N) content; C/N ratio; labile phosphorus (P), inorganic NaOH-extractable P and total NaOH-extractable P. The pairs were G1-M1; G2-M2, and G3-M3. Dominance refers to the dominance of *G. dewevrei* in terms of above-ground biomass measuring in 2005. The values of the soil parameters (except extractable inorganic P and total extractable P) are the average from 3 locations within the plot, with 95% confidence intervals at $P = 0.05$. The values of extractable inorganic P and total extractable P are the average from 2 locations within the plot, with standard deviations (Detail available from KSH on request).

Forest Types	Plot	Number of Tree Species	Fisher's Alpha	Dominance (%)	Basal Area (m^2 ha^{-1})	Top Soil (0–30 cm)						
						pH	C (%)	N (%)	C/N	Labile P (ppm)	Inorganic NaOH-Extractable P (ppm)	Total NaOH-Extractable P (ppm)
Monodominant	G1	33	9.37	73	33.45	3.72 ± 0.05	1.80 ± 0.59	0.15 ± 0.04	11.90 ± 0.64	0.05 ± 0.03	1.96 ± 0.28	4.08 ± 0.05
	G2	35	9.71	85	30.74	3.61 ± 0.12	1.59 ± 0.45	0.13 ± 0.03	11.67 ± 0.62	0.06 ± 0.03	1.18 ± 0.22	3.31 ± 0.40
	G3	39	10.98	97	31.87	3.75 ± 0.05	2.69 ± 0.46	0.18 ± 0.03	13.30 ± 0.77	0.09 ± 0.03	0.98 ± 0.03	3.25 ± 0.13
Mixed	M1	107	45.65	0	23.71	3.67 ± 0.05	2.12 ± 0.03	0.18 ± 0.01	11.93 ± 0.53	0.07 ± 0.03	1.69 ± 0.09	4.64 ± 0.47
	M2	130	59.19	0	26.38	3.74 ± 0.21	1.74 ± 0.47	0.16 ± 0.03	11.01 ± 0.64	0.06 ± 0.03	1.10 ± 0.38	3.32 ± 0.67
	M3	104	45.13	0	23.19	3.72 ± 0.14	1.82 ± 0.37	0.16 ± 0.03	11.42 ± 0.19	0.08 ± 0.03	1.01 ± 0.06	2.87 ± 0.34

standing crop dry mass by collecting all leaf litter in an area of equal dimension to the litter trap (i.e. 0.5 m × 0.5 m) and drying it to constant mass, four times (Apri 2007, Jul 2007, Sep 2007 and Jan 2008), and calculated the average. Decomposition rates for the quadrats were estimated as the dry mass of leaf litter fall (Mg ha^{-1} yr^{-1}; mean of three litter fall traps) divided by the dry mass of leaf standing crop on the forest floor (Mg ha^{-1}), *sensu* Schlesinger (1991). In total, decomposition rates for nine quadrats in each forest type were calculated, and we compared the two forest types using 95% confidence intervals ($n = 3$; for reasons of using sets of confidence intervals for comparison see Cherry 1988). The decomposition rates were then correlated with the respective tree diversity index ($n = 9$) for each forest type using a non-parametric Spearman rank test with significance level set at 0.05.

Litter bag experiments

We compared the decomposition rates of litter mixtures of air-dried organic *L. nobilis* (hereafter bay leaves) and newly senescent *G. dewevrei* leaves (hereafter *Gilbertiodendron* leaves) with those of the single-species litters of the respective species, in both monodominant forest and mixed forest, using litter bags. We placed five bay leaf litter bags, five *Gilbertiodendron* litter bags and five mixed litter bags in each of ten randomly selected quadrats in each of six plots at the beginning of the wet season in Apri 2008. All litter bags were placed randomly within the quadrats, at least 5 m from the quadrat perimeter, and pinned to the ground in contact with the soil surface. We retrieved one 'set' of litter bags (one bay, one *Gilbertiodendron* and one mixed litter bag; randomly chosen) from each quadrat after 1, 3, 5, 7 and 9 mo. After collection, all bag contents were oven-dried (55 °C) to constant weight (±0.01 g). Decomposition was calculated as the percentage of initial litter mass lost. To determine the individual species responses to the litter mixtures, mixed samples were separated into species and reweighed. In total, the data set is based on 60 quadrats, 30 located in monodominant and 30 in mixed species forest, five collection periods, and a total of 900 litter bags (300 each of bay, *Gilbertiodendron* and mixed species bags).

The litter bag (10 cm × 15 cm, 2-mm mesh) was made of nylon netting sewn with polyester thread and filled with 4.0 g of leaves, or 2.0 g of each species in the mixed bags. An additional batch of litter bags containing standard substrates (bay leaves, $n = 15$; *Gilbertiodendron* leaves, $n = 15$) was oven-dried (55 °C) and weighed to develop conversion factors to express the initial weights of leaf samples in the litter bags as dry mass. We used bay leaves and *Gilbertiodendron* leaves as the standard substrates for three practical reasons. First, bay leaves are easily available and are a common standard substrate used in a recent pan-tropical study (Powers et al. 2009), and *Gilbertiodendron* leaves are easy to obtain because *G. dewevrei* dominates the mono-dominant forests of the study sites. Second, these two substrates vary in initial litter quality even though they have similar N content (1.9%), C content (48–49%) and the same C/N ratio (25 and 26; Table 2). *Gilbertiodendron* leaves, the relatively lower-quality species, are thick, with a high crude fibre (cellulose and lignin) concentration of 63.5% (Gross et al. 2000), whereas bay leaves are higher quality, with a relatively lower crude fibre concentration of 46.8% (Kutbay 2000). Although we do not have the lignin/N ratio, another measure of leaf quality that can control decomposition dynamics (Melillo et al. 1982) for both species, *Gilbertiodendron* leaves have approximately 11 times the phenolic concentration of bay leaves (Gross et al. 2000; Powers et al. 2009), suggesting that *Gilbertiodendron* should decompose more slowly than bay. Both substrates differed considerably in colour, texture and characteristics of epidermis and leaf veins, therefore allowing each species in the mixed species litter to be accurately separated and weighed.

For each quadrat, we calculated the decomposition rate, *k*, of the two substrate species in single species and mixed species bags by fitting an exponential decay model to the changes in remaining leaf mass over time:

$$X = 100e^{-kt}$$

where X is the proportion of initial leaf mass remaining at time t (in months); and k is the exponential decay coefficient (Wieder & Wright 1995; modified from Olson 1963). This model is considered to be biologically meaningful because it corresponds to our current understanding of the litter breakdown process, with initially rapid decay due to the leaching of water-soluble and easily degraded compounds and slower loss of the remaining more recalcitrant material over time (Jenny et al. 1949; Melillo et al. 1982; McClaughterty et al. 1985; Rubinstein & Vasconcelos 2005). Subsequently, we compared decomposition k-values of the substrates in different treatments and forest types using 95% confidence intervals. We also compared the predicted decomposition rate of the mixed litter (i.e. arithmetic mean of the two component species) with the observed decomposition rate of the mixed litter as a whole. Finally, we correlated decomposition k-values with the tree diversity index within each forest type to determine if

Table 2. Leaf chemistry – C (%), N (%), C/N ratio, P (mg kg^{-1}) and C/P ratio – and wood density of the two species used in litter experiments and some early and late successional species from mixed forests in Dja faunal reserve. Data on the *Gilbertiodendron dewevrei* and mix-forest species was obtained from the voucher specimen collected by SLL. Data on bay leaves (*Laurus nobilis*) was obtained from Peñuelas & Estiarte (1997).

Species	No. of Samples	C (%)	N (%)	C/N ratio	P (mg kg^{-1})	C/P ratio	Wood Density (g cm^{-3})
Litter Bag Experiments							
Laurus nobilis L.		49.22	1.94	25.4			
Gilbertiodendron dewevrei (De Wild.) J. Léonard	18	47.84	1.85	26.0	1160.0	0.04	0.71
Early Successional Mixed Forest Species							
Allanblackia floribunda Oliv.	2	48.62	1.63	29.7	766.0	0.06	0.72
Antidesma lacinatum Müll.Arg.	1	46.69	1.42	32.9	755.0	0.06	0.61
Late Successional Mixed Forest Species							
Calpocalyx dinklagei Harms	2	48.48	1.46	33.2	887.0	0.05	0.65
Carapa procera DC.	2	48.36	2.96	16.3	630.0	0.08	0.63
Celtis tessmanni Rendle	1	49.81	1.46	34.1	1117.0	0.04	0.66
Dalium guineensis Wild.	1	49.54	1.81	27.3	769.0	0.06	0.89
Diospyros holyeana F. White	1	48.88	2.25	21.7	962.0	0.05	0.83
Lepidobotrys staudtii Engl.	1	48.96	1.81	27.0	916.0	0.05	
Maranthes glabra (Oliv.) Prance	1	50.44	2.74	18.4	554.0	0.09	0.88
Piptaniastrum africanum (Hook.f.) Brenan	1	44.10	3.59	12.3	988.0	0.04	0.61
Plagiostyles africana (Müll.Arg.) Prain	2	47.59	2.25	21.2	942.0	0.05	0.75
Polyalthia suavolens Engl. & Diels	1	47.52	1.48	32.2	783.0	0.06	0.70
*Strombosiopsis tetandra*Engl.	1	48.59	2.88	16.9	1273.0	0.04	0.67
Syncepalum dulcificum(Schum.) Baill.	4	47.62	1.78	26.8	891.0	0.05	0.68
*Tessmannia africana*Harms	1	48.61	2.10	23.1	1724.0	0.03	0.84
*Vitex grandifolia*Gürke	1	46.32	2.90	16.0	2018.0	0.02	0.53
*Xylopia staudtii*Engl. & Diels	1	47.70	2.55	18.7	959.0	0.05	0.44
Average (late successional species only)		48.17	2.27	23.0	1027.5	0.05	0.70
Confidence Interval (95%)		±0.77	±0.33	±3.5	±196.6	±0.01	±0.07

a tree diversity effect was observed on the two substrate species.

One potential bias in a litter bag experiment is that soil particles, extraneous debris and roots may enter the bag over time and affect the accuracy of measurement of mass loss. Therefore, we washed the litters in water and removed all sample content, using fine tweezers, into labelled envelopes before oven drying. Thus, any problems associated with soil contamination of the processed litters were minimized.

For the litter bag experiments, we used a non-parametric Spearman rank test for all correlation tests that involved the tree diversity index and, in cases of multiple comparisons, we applied the Bonferroni correction (Rice 1989). All statistical tests were conducted using SPSS 13.0 statistical software, and the significance level was set as 0.05.

Results

Observations in two forest types

For the three plots in monodominant forest, the average leaf-only litter fall dry mass collected was 7.31 (1 Mg = 1 metric tonne = 1 × 10^6 g), 6.53 and 5.22 Mg ha^{-1} (n = 30; i.e. ten quadrats per monodominant forest plot with three traps in each quadrat). For the three plots of mixed forest, the average leaf litter fall dry mass was 9.27, 10.28 and 9.35 Mg ha^{-1} (n = 30; i.e. ten quadrats per mixed forest plot with three traps in each quadrat). On average, the monodominant forest produced 6.36 ± 1.20 Mg dry mass ha^{-1} of leaf-only litter fall per annum (n = 3 plots) whereas the mixed forest had 9.63 ± 0.64 Mg dry mass ha^{-1} (n = 3 plots). The mean of paired differences in leaf-only litter fall mass between the two forest types was 3.28 ± 1.31 Mg dry mass ha^{-1}, showing that the mixed forest had higher leaf production than the monodominant forest.

In monodominant forest, the average litter standing crop (dry mass) from the four collections throughout the year was 8.97, 8.02 and 8.15 Mg ha^{-1} (n = 3 for each plot), and in the mixed forest 3.26, 3.82 and 3.52 Mg ha^{-1} (n = 3). On average, the monodominant forest had a significantly higher litter standing crop mass (8.38 ± 0.58 Mg ha^{-1}) as compared to the mixed forest (3.53 ± 0.32 Mg ha^{-1}). The mean of paired differences between the two forest types was 4.85 ± 0.88 Mg ha^{-1}. The average estimated decomposition rate, using the litter fall/standing crop ratio, in mixed forest (3.40 ± 0.31) was significantly higher than that in the monodominant forest (0.80 ± 0.15).

The proportions of the total annual leaf litter fall in the three monodominant forests belonging to *G. dewevrei* were 52%, 75% and 92%, respectively (average proportion: 73 ± 23%; n = 3 plots). The abundance of *Gilbertiodendron* leaves as a proportion of total litter fall was negatively correlated with the tree species diversity at the quadrat scale (Spearman rank coefficient = −0.35, $P < 0.05$, one-tailed).

Simpson's tree diversity index of the nine quadrats from monodominant forests with estimated decomposition rates ranged from 1.15 to 4.17, with no overlap to the diversity of the nine quadrats from mixed forests, which ranged from 5.12 to 16.89. Leaf decomposition rate was not significantly correlated with Simpson's tree diversity within each forest type when analysed separately (Fig. 2a, b).

Mixed litter decomposition experiments

We fitted an exponential curve to the calculated remaining dry mass of leaves of (1) bay, (2) *Gilbertiodendron*, (3) mixtures of the two, from the litter bags collected over 9 mo in each of the two environments (mixed and monodominant forests). The six data sets each fitted the exponential function relatively well (all $R^2 \geq 0.8$).

The higher quality bay leaves had higher decomposition rates than the *Gilbertiodendron* leaves throughout the experiment, regardless of being in single species or mixed species bags, or being in monodominant or mixed forest (Fig. 3a, b; Table 3). Overall, after 9 mo in monodominant forest, 73% and 34% mass losses were observed for bay and *Gilbertiodendron* leaves, respectively, averaged over all

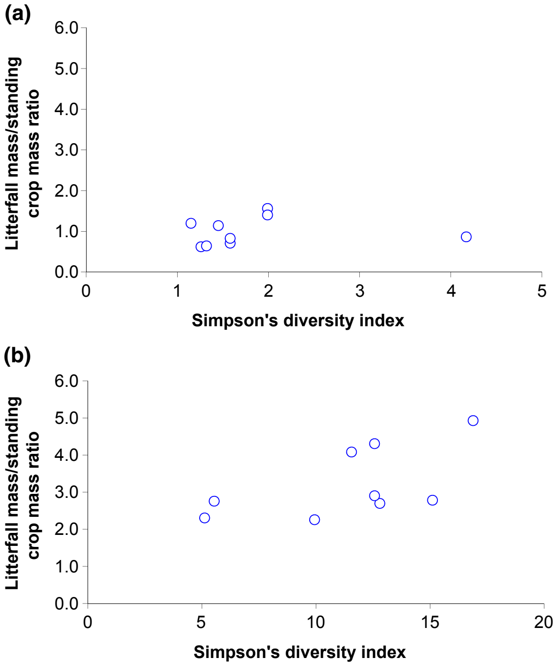

Fig. 2. Leaf litter fall/standing crop ratio is not significantly correlated with Simpson's tree diversity index ($P > 0.05$) when data was analysed separately for the monodominant *Gilbertiodendron* forest (**a**), and mixed forest (**b**) using non-parametric Spearman's rank correlation test.

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replicates. Over the same experimental period in mixed forest, decomposition of 77% mass loss for bay and 31% mass loss for *Gilbertiodendron* leaves was observed.

Consistent with percentage litter loss analyses (Fig. 3a, b), decomposition *k*-values for *Gilbertiodendron* and bay litters did not significantly differ between monodominant and mixed forests (Table 3). However, the decomposition *k*-values for *Gilbertiodendron* litter differed significantly when we compared treatment types in the mixed forest (Table 3). The decomposition *k*-values of *Gilbertiodendron* litter of mixed litter bags in the mixed forest were significantly higher than those of the single-species bags in the mixed forest. In addition, the decomposition *k*-value of bay leaves in mixed litter bags in the mixed forest was significantly higher as compared to the single bay litter in monodominant forest (Table 3). Nevertheless, decomposition *k*-values of each litter species were not correlated with the tree species diversity index, either in single species or mixed litter bags in either forest type (Fig. 4a, b).

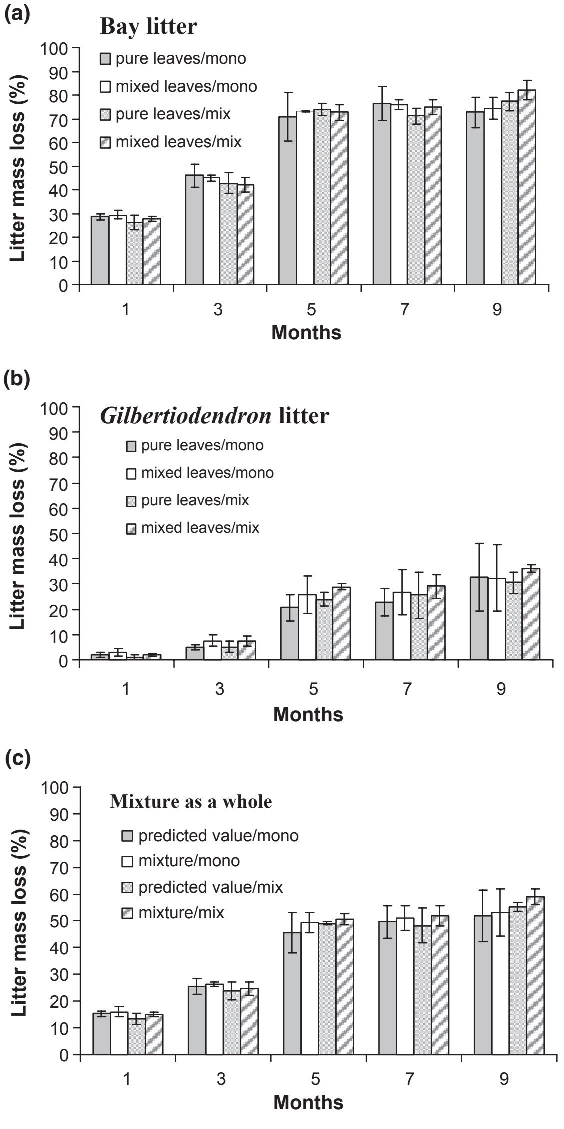

Fig. 3. Litter mass loss (%) of bay (**a**) and *Gilbertiodendron* leaves (**b**) in monodominant forest (mono; $n = 3$) and mixed forest (mix; $n = 3$) over 9 mo. Single-species treatment is denoted as pure leaves and mixed-litter treatment is mixed leaves. Litter mass loss (**c**) was also measured in litter mixtures as a whole (mixture) compared with the average of both the bay and *Gilbertiodendron* litter individual losses (predicted value). The bars shows the 95% confidence intervals at $P = 0.05$.

The forest type had no impact on decomposition of the two litter types. Both high-quality bay leaves and low-quality *Gilbertiodendron* leaves experienced rapid early decay during the first 5 mo, after which the decomposition rates drastically reduced in both forest types (Fig. 3a, b). For each species in the single-species bags, there was no difference in decomposition between the two forest types throughout the experimental period (Fig. 3a, b). After 9 mo, the predicted litter losses of the mixed litter in monodominant and mixed forests were 51.9 ± 9.8% ($n = 3$) and 55.2 ± 1.8% ($n = 3$), respectively. These values were not significantly different from those observed in mixed litter as a whole in monodominant (53.3 ± 8.8%; $n = 3$) and mixed forests (59.0 ± 2.8%; $n = 3$; Fig. 3c).

Decomposition patterns over time between single-species bags and the corresponding species from the mixed bags did not differ for bay leaves. However, *Gilbertiodendron* leaves from the mixed bags in the mixed forest collected after 5 and 9 mo decomposed significantly faster than those in the single-species bags (Fig. 3b). Interestingly, the mixed litter effect was not detectable in the mixed litter as a whole but was observed only when the individual leaf species was examined. However, this significant positive, litter diversity effect was not observed in the collections after 1 and 7 mo, although nine out of ten pair-wise comparisons, regardless of forest type, showed that the decomposition rate of *Gilbertiodendron* in the mixed bag was greater than when used alone in a bag (Fig. 3b).

Discussion

Observational evidence on litter quality impact on decomposition

Calculated forest floor decomposition rates were much greater in the higher diversity, mixed forest than the adjacent lower diversity, monodominant forest. This had two proximate causes: the mixed forest had both a greater mass of leaf litter fall and a lower litter standing crop mass than the monodominant forest. On average, the mixed forest produced 54% more leaf litter fall and its leaf litter decomposed four times faster than the

Table 3. The decomposition rates (k) of bay and *Gilbertiodendron* litter in both the single-species litter bags and mixed litter bags observed in the monodominant (n = 3) and mixed forest (n = 3). CI (95%) is the 95% confidence intervals at P = 0.05; CI (90%) is the 90% confidence intervals at P = 0.10.

Litter Types	Forest Types	Treatment	k (yr^{-1})	CI (95%)	CI (90%)
Bay	Monodominant	Pure	1.92	1.69–2.15	1.73–2.11
		Mixed	1.96	1.69–2.23	1.73–2.19
	Mixed	Pure	2.20	2.01–2.38	2.04–2.35
		Mixed	2.63	2.16–3.10	2.24–3.02
Gilbertiodendron	Monodominant	Pure	0.68	0.40–0.97	0.44–0.92
		Mixed	0.68	0.35–1.03	0.39–0.98
	Mixed	Pure	0.52	0.46–0.59**	0.47–0.58*
		Mixed	0.65	0.64–0.66**	0.64–0.66*

*indicates that the treatments within the same forest types are significantly different at 0.10 level.

**indicates that the treatments within the same forest types are significantly different at 0.05 level.

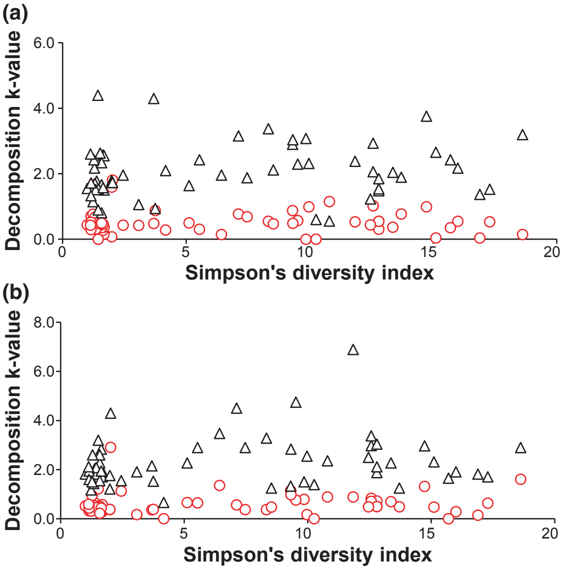

Fig. 4. Decomposition k-values for *Gilbertiodendron* litter (circles) and bay litter (triangles) from single-species litter bags (**a**) and mixed litter bags (**b**) are not significantly correlated with Simpson's tree diversity index ($P > 0.05$) in both monodominant and mixed forests. Simpson's tree diversity index for the monodominant forests ranged from 1.15 to 4.17, with no overlap with the tree diversity of mixed forests that ranged from 5.12 to 16.89. The tree diversity-decomposition relationship was analysed for each forest type separately.

monodominant counterpart. This is despite the apparently indistinguishable soil properties, topography and climate of the monodominant forest of *G. dewevrei* and the adjacent high-diversity forest in both the Democratic Republic of the Congo (Hart 1985; Hart et al. 1989; Conway 1992) and the plots studied here (Peh et al. 2011b). Our result highlights the potential impact of individual species on productivity and decomposition.

The high litter fall and low standing litter crop in mixed compared to monodominant forests is in agreement with previous observations from both monodominant and mixed forests in the Democratic Republic of the Congo (Torti et al. 2001). More specifically, the large proportion of the leaf litter fall produced by the monodominant species, combined with slow decomposition of the leaves, has been hypothesized as one of the key traits that leads to the modification of the understorey environment so as to prevent establishment of other species, and thus attain and perpetuate their dominance (Torti et al. 2001).

Although it has long been claimed that decomposition rates are determined by a suite of hierarchically organized factors, from climate to soil, litter quality and fauna diversity (e.g. Swift et al. 1979; Lavelle 1993), we found significantly different decomposition rates at sites on the same soil type, but no difference in decomposition rates with variation in tree diversity, indicating that factors such as soil and litter quality, which drive decomposition, may not be inherently correlated with tree species diversity. Nevertheless, litter decomposition was slower in the monodominant forests, which had two major implications. First, because an average of 73% of the total annual leaf litter fall in the monodominant forests belonged to *Gilbertiodendron*, the natural dominance of a single species with low litter quality appears to be the primary mechanism responsible for the lower decomposition rates; however this does not explain the difference in litter production between monodominant and mixed forests. Second, the tree diversity effect may depend on the range of the species diversity gradient studied and may only be detectable if the diversity range is sufficiently wide and sample sizes are sufficiently large. Thus, we cannot rule out the possibility that the lack of strong correlation between diversity and decomposition rate within each forest type was due to narrow diversity range and small sample size.

It has been suggested that decomposition rates may be influenced by interaction among many variables, such as environmental conditions (Meentemeyer 1984) and soil fauna (Heneghan et al. 1999). Nevertheless, there is little evidence that soil properties were significantly different between our monodominant and mixed forest plots

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(Table 1; for details see Peh et al. 2011b). Likewise, the plots of the two forest types experienced similar climatic conditions (for details see Peh et al. 2011b). We can, therefore, rule out major influences of soil and climatic on the differences in decomposition rates between our monodominant and mixed forest quadrats.

Alternatively, it has been suggested that decomposition dynamics may be directly linked to the successional status of a tree species – early-successional tree species may tend to have high-quality litter (fast decomposition) while late-successional tree species may tend to have low-quality litter (see Pastor & Post 1986). Although the contrast between late-successional *Gilbertiodendron* (*k*-value = 0.5–0.6 yr^{-1}) and the early-successional species (e.g. *Celtis zenkeri*, *k*-value = 4.18 yr^{-1}) is consistent with the analysis of Pastor & Post (1986), more evidence is needed to support this view because: (1) extensive theoretical and empirical work on *Gilbertiodendron* forest and its adjacent mixedforest have shown that one of these two forest types is unlikely to be a variety of earlier successional states of the other (e.g. Connell & Lowman 1989; Hart et al. 1989; Torti et al. 2001), notably, the mixed forest is the typical Central African plateau evergreen moist forest covering millions of hectares across the Congo Basin; and (2) there are examples of late-successional species with high-quality litter (low C/N ratio) and early-successional species with poor-quality litter (high C/N ratio) (Table 2). Furthermore, as higher wood density is often used as a proxy for late-successional species, there is no significant correlation between wood density and litter quality (Fig. 5a, b) based on the species listed in Table 2 (although there is a hint of a relationship).

We did not conduct surveys on the decomposer communities in our quadrats when the experiments were carried out. Since we do not have data on soil fauna, we cannot address the biotic variables affecting decomposition. Nonetheless, the mixed litter in mixed forest may have had a more diverse decomposer community (Torti et al. 2001), and did show marginally significantly more rapid decomposition compared to that in monodominant forest (Table 3). Further research is required.

Experimental evidence on effects of litter mixture

Our observed bay and *Gilbertiodendron* litter decomposition rates, expressed as exponential decay *k*-values, are 1.9–2.6 yr^{-1} and 0.5–0.6 yr^{-1}, respectively. The decomposition rates of bay litter were >1.0 yr^{-1}, typically in the range found for tropical forests (Didham 1998; Scherer-Lorenzen et al. 2007) and other reported tropical African forest species (e.g. *Ceiba pentandra*, 2.16 yr^{-1}; *Cola lepidota*, 2.18 yr^{-1}, *Desbordesia glaucescens*, 1.60 yr^{-1}; Songwe et al. 1995). In contrast, decomposition rates of the *Gilbertiodendron* litter were <1.0 yr^{-1} but comparable to the 0.6–0.7 yr^{-1} of another monodominant species, e.g. *Peltogyne gracilipes*, in the Neotropics (Villela & Proctor 2002).

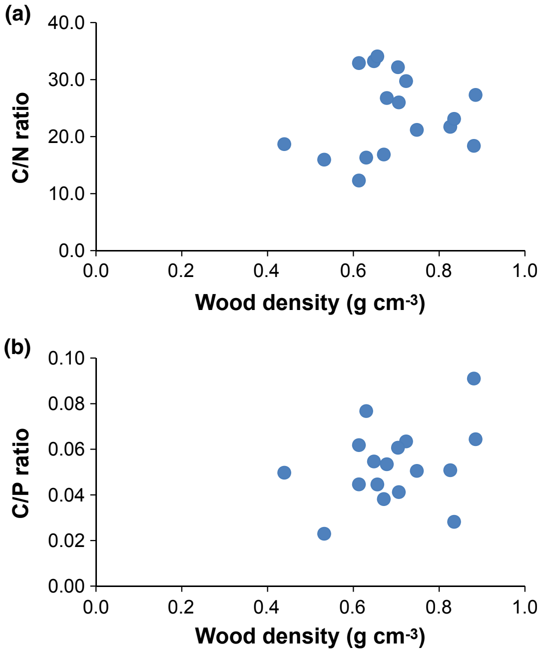

Fig. 5. Scatterplots of C/N ratio (**a**) and C/P ratio (**b**) along gradient of wood density based on the species data in Table 2. No significant relationships were observed between C/N ratio and wood density ($P > 0.05$). Likewise, there is no correlation between C/P ratio and wood density ($P > 0.05$).

Our finding that each standard litter species had the same decomposition rate in the two contrasting forest types appears to contradict our direct observations that litter in the mixed forest decomposed four times faster than that in the monodominant forest (Table 4). The reason is likely compositional differences in terms of litter species between the two forest types. Even though this study was designed with the aim of investigating whether decomposition rate of monodominant forest (K_{mono}) and that of mixed forest (K_{mix}) are different, using standard species of different initial litter quality, a new calculation of the K_{mix}/K_{mono} ratio based on the experimental data with known proportions of *Gilbertiodendron* leaves on the monodominant forest floor, shows that the difference in decomposition rates between the two forest types was about three-fold (Table 4). Thus, the apparent discrepancy between the estimated decomposition rates from direct observation and those from litter bag experiments can be reconciled. The three- to four-fold difference in decomposition rates between the monodominant and mixed forests observed is likely due, in large part, to differing species composition of the litter, and particularly the dominance of slow-

Table 4. Decomposition rates (k yr^{-1}) from the three pairs of 1 ha forest plots at the Dja Faunal Reserve, derived from the ratio of litter fall mass to standing crop, and from the litter bag experiments. The pairs were G1-M1; G2-M2, and G3-M3.

	Plot					
	G1	M1	G2	M2	G3	M3
Litter Fall Mass/standIng Crop Ratio	0.65	3.29	0.91	3.21	0.84	3.72
Ratio Between Pair		5.04		3.54		4.45
Average (n = 3)						4.34
Bay Litter						
Single-Species Bag	2.05	2.01	2.03	2.31	1.69	2.26
Mixed Bag	2.21	2.41	1.73	3.10	1.93	2.37
Gilbertiodendron Litter						
Single-Species Bag	0.95	0.59	0.44	0.49	0.67	0.49
Mixed Bag	0.97	0.65	0.36	0.66	0.72	0.64
Proportion of *Gilbertiodendron*	52.0	0.0	75.0	0.0	92.0	0.0
*K_{mix}/K_{mono}		1.54		4.41		2.90
Average (n = 3)						2.95

*New calculation for the ratio of decomposition rate of mix forest (k_{mix}) to decomposition rate of monodominant forest (k_{mono}) based on litter bag experiment data. For example, k_{mix}/k_{mono} ratio of the G3-M3 pair is:

$$\begin{aligned} k_{mix}/k_{mono}\ \text{ratio} &= k_{mix}/(P_g \times k_{gm}) + (P_{ng} \times k_{bm}) \\ &= 2.37/(0.92 \times 0.72) + (0.08 \times 1.93) \\ &= 2.90 \end{aligned}$$

where k_{mix} is the average decay rate of the bay leaves in the mixed bags in mixed forests; P_g and P_{ng} are the average proportions of *Gilbertiodendron* and non-*Gilbertiodendron* leaves on the monodominant forest floor, respectively; k_{gm} is the average decay rate of the *Gilbertiodendron* leaves in the mixed bags in monodominant forests; and k_{bm} is the average decay rate of the bay leaves in the mixed bags in monodominant forests.

decomposing *Gilbertiodendron* leaves. Hence, decomposition differences amongst our forest plots appears largely determined by the presence or absence of *G. dewevrei*.

The similarity in the litter bag decomposition rate does not necessarily mean that these forest types share the same biotic conditions. For example, Torti et al. (2001) noted lower numbers of leaf litter arthropods in an African monodominant forest compared to a mixed forest, even though there was considerable overlap among the orders represented between the two forest types. These orders included acari, coleoptera, hymenoptera, isopoda, snails and spiders. One possible explanation for the similar decay rates across different forest types is the exclusion of macroarthropods in our study. We recognize that the small mesh size of the litter bags may have excluded the larger soil invertebrates such as earthworms, millipedes and snails that can potentially process large amounts of leaf litter. Although we did find microarthropods in the litter bags, a lack of macrofauna may lead to a failure to detect differences in decomposition rates between the two forest types if the macrofauna differs. Nevertheless, the similar decomposition k-values across the two forest types does appear to reflect that the abiotic and microbial environments were likely similar among the forest sites.

There was a clear temporal pattern in rates of decomposition for the two standard litter types, both of which decreased drastically after 5 mo both forest types. This is a typical pattern of litter decomposition described using the exponential decay model. Our litter bag experiment started at the beginning of the wet season, thus rain likely facilitated the leaching of water-soluble compounds and washed away the easily degraded compounds in the litter. The remaining material after 5 mo was the recalcitrant parts of the leaves. However, the exclusion of macrofauna in our study might also have slowed down the loss of recalcitrant material after 5 mo.

Our results confirm the findings from previous studies that leaf species of high litter quality have higher decomposition rates than those of low litter quality (e.g. Melillo et al. 1982; Heal et al. 1997; Hector et al. 2000; Hättenschwiler et al. 2005). Consistent with other studies showing that high-quality litter may influence the decomposition of low-quality litter (see Hättenschwiler & Gasser 2005), we also found that the low-quality litter does break down faster when mixed with high-quality litter over a longer temporal scale. The *Gilbertiodendron* leaves of the litter mixture in mixed forests collected after 5 and 9 mo exhibited positive, non-additive effects of litter mixing on decomposition (Fig. 3). However, this mixing effect was not observed in litter mixtures collected after 1, 3 and 7 mo. This confirms that the duration of decomposition experiments is a crucial component of their interpretation. Therefore, results from experiments that examined only short-term decomposition must be interpreted with caution. In addition, the lack of evidence of faster breakdown of mixed *Gilbertiodendron* litter in monodominant forest suggests that the litter composition effect may be context-dependent. The forest floor composition apparently had a larger effect on litter bag decomposition than the composition within the litter bags themselves.

In terms of decomposition k values, the effect of mixed litter is significant when we compare the decay rate of *Gilbertiodendron* litter from single-species bags with that from mixed bags in the mixed forest. Furthermore, the interplay between forest type (i.e. mixed forest) and litter composition (i.e. mixed litter) may enhance breakdown of the high-quality litter type. This is suggested by comparison of the decomposition k-values of bay litter in the mixed forest–mixed litter combination with the bay litter of single-species bags in the monodominant forest

(Table 4). This implies that litter mixing effects on decomposition may only manifest between quadrats with significant differences in terms of plant diversity indices, specifically when the higher diversity litter includes species with higher litter quality. This is broadly consistent with a study using temperate species, which found a positive effect on litter nutrient release when litter composition and microenvironment (induced by the plant diversity) were known to interact (Blair et al. 1990). Nevertheless, the magnitude of such influence found in our study was small. Tree diversity effects on decomposition rates on bay and *Gilbertiodendron* leaves were not detected. This may be due to the inaccessibility of our experimental litter to the larger soil decomposers that are known to alter leaf litter mixing effects on decomposition (Hättenschwiler & Gasser 2005).

Our study is consistent with the results of other litter bag experiments that report significant effects of litter mixtures on decomposition rates (see Gartner & Cardon 2004 for details). However, current knowledge does not allow us to explain why contrasting results of negative, positive or neutral effects of litter diversity on decomposition rates occurred in the various studies. Our study suggests that the effects of litter mixtures may be context-dependent, and may differ among different ecosystems (also see Jonsson & Wardle 2008). Nevertheless, our study demonstrates a mechanistic insight that helps explain differences in decomposition between a mixed species forest and a natural monodominant forest: a single species can have a dominant effect on litter decomposition within an ecosystem via a specific trait (i.e. low-litter quality), and an increase in species richness may then dilute the influence of the dominant species.

Limitations

We used equal proportions of two litter species with differing functional properties (i.e. high- and low-litter quality) in the mixed bags. An alternative methodology would be to use species in the proportions in which they occurred in the forests (Hector et al. 2000). Although litter decay is affected by the quality and quantity of litter from different species (Chapman et al. 1988), the approach of Hector et al. (2000) is unfortunately very challenging in the setting of a tropical forest where litter species composition is (a) difficult to assess accurately and (b) difficult to assemble for placement into 600 litter bags, given the high diversity of the regional species pool. Actual proportions of species present vary among forest types and within forest types over short distances, as overlying tree diversity differs. However, one limitation of our study was that we used bay leaves as our high-quality litter, which do not occur naturally at our site, so we cannot conclude whether bay correctly reflects decomposition rates of the non-dominant forest species in the monodominant forest or those of species found in the mixed forest. However, experiments using bay leaves have been conducted in a pan-tropical study (except Africa; see Powers et al. 2009) and their results might be useful here for comparison, where there is no naturally occurring species overlap. Similarly, it is unclear if *Gilbertiodendron* leaves represent the most recalcitrant litter in the mixed forest, without having more data. Thus, our study can only provide an estimate of the relative decomposition rates of high-quality and low-quality litters in the two forest types.

We used only two species for our litter mixture decomposition experiments and compared this with the expected value on the basis of single-species decomposition. This limits a thorough assessment of the litter composition effects and restricts a general description of leaf litter decomposition as a function of litter diversity (Hättenschwiler et al. 2005), but logistical considerations led to this limitation. Nevertheless, this study provides valuable insights on the effect of litter mixing (i.e. mixture of low-quality and high-quality litters) and is, to our knowledge, the first litter mixture experiment to be conducted in a natural, tropical lowland forest. Also, our standard litter species enables our results to be directly comparable between the two forest types within the study area and other comparative studies (e.g. Powers et al. 2009). Furthermore, our use of only two species in the experiment facilitated the separation of decomposition rates among species within mixtures. This approach is important because the mass loss measured in a litter mixture may mask species-specific responses, as shown in our results (Fig. 3).

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References

Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystem; a triangular relationship. *Oikos* 79: 439–449.

Bernhard-Reversat, F. 1998. Changes in relationships between initial litter quality and CO_2 release during early laboratory decomposition of tropical leaf litter. *European Journal of Soil Biology* 34: 117–122.

Bernhard-Reversat, F. & Schwartz, D. 1997. Change in lignin content during litter decomposition in tropical forest soils (Congo): comparison of exotic plantations and native stands. *Comptes Rendus de l'Acadèmie des Science Paris, Science de la Terre et des Planètes* 325: 427–432.

Blair, J.M., Parmelee, R.W. & Beare, M.H. 1990. Decay rates, nitrogen fluxes, and decomposer communities of single- and mixed-species foliar litter. *Ecology* 71: 1976–1985.

Bradshaw, C.J.A., Navjot, N.S. & Brook, B.W. 2009. Tropical turmoil: a biodiversity tragedy in progress. *Frontiers in Ecology and Environment* 7: 79–87.

Chapman, K., Whittaker, J.B. & Heal, O.W. 1988. Metabolic and faunal activity in litters of tree mixtures compared with pure stands. *Agriculture, Ecosystems and Environment* 24: 33–40.

Chave, J., Condit, R., Muller-Landau, H.C., Thomas, S.C., Ashton, P.S., Bunyavejchewin, S., Co, L.L., Dattaraja, H.S., Davies, S.J., Esufali, S., Ewango, C.E.N, Feeley, K.J., Foster, R.B., Gunatilleke, N., Gunatilleke, S., Hall, P., Hart, T.B., Hernandez, C., Hubbell, S.P., Itoh, A., Kiratiprayoon, S., LaFrankie, J.V., de Lao, S.L., Makana, J.R., Noor, M.N.S., Kassim, A.R., Samper, C., Sukumar, R., Suresh, H.S., Tan, S., Thompson, J., Tongco, M.D.C., Valencia, R., Vallejo, M., Villa, G., Yamakura, T., Zimmerman, J.K. & Losos, E.C. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. *Plos Biology* 6: 455–462.

Cherry, S. 1988. Statistical tests in publications of The Wildlife Society. *Wildlife Society Bulletin* 26: 947–953.

Connell, J.H. & Lowman, M.D. 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. *American Naturalist* 134: 88–119.

Conway, D.J. 1992. *A comparison of soil parameters in monodominant and mixed forest in the Ituri Forest Reserve, Zaire*. BSc (Hons) Thesis. University of Aberdeen, Aberdeen, UK.

Coûteaux, M.M., Bottner, P. & Berg, B. 1995. Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution* 10: 63–66.

Didham, R.K. 1998. Altered leaf-litter decomposition rates in tropical forest fragments. *Oecologia* 116: 397–406.

Gartner, T.B. & Cardon, Z.G. 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos* 104: 230–246.

González, G. & Seaastadt, T.R. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* 82: 955–964.

Gross, N.D., Torti, S.D., Feener, D.H. Jr & Coley, P.D. 2000. Monodominance in an African Rain Forest: is reduced herbivory important? *Biotropica* 32: 430–439.

Hart, T.B. 1985. T*he ecology of a single-species-dominant forest and of a mixed forest in Zaire, Africa*. PhD Thesis. Michigan State University, MI, US.

Hart, T.B., Hart, J.A. & Murphy, P.G. 1989. Monodominant and species-rich forests in the humid tropics: causes for their co-occurrence. *American Naturalist* 133: 613–633.

Hättenschwiler, S. & Gasser, P. 2005. Soil animals alter plant litter diversity effects on decomposition. *Proceedings of National Academy of Sciences USA* 102: 1519–1524.

Hättenschwiler, S., Tiunov, A.V. & Scheu, S. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution and Systematics* 36: 191–218.

Heal, O.W., Anderson, J.M. & Swift, M.J. 1997. Plant litter quality and decomposition: an historical overview. In: Cadish, G. & Giller, K. E. (eds). *Driven by nature: plant litter quality and decomposition*. pp. 3–32. CAB International, Wallingford, UK.

Hector, A., Beale, A.J., Minns, A., Otway, S.J. & Lawtin, J.H. 2000. Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. *Oikos* 90: 357–371.

Heneghan, L., Coleman, D.C., Zou, X., Crossley, D.A. & Haines, B.L. 1999. Soil microarthropod contributions to decomposition dynamics: tropical–temperate comparisons of a single substrate. *Ecology* 80: 1873–1882.

Jenny, H.G., Gessel, S.P. & Bingham, F.T. 1949. Comparative study of decomposition of organic matter in temperate and tropical regions. *Soil Sciences* 68: 419–432.

Jonsson, M. & Wardle, D.A. 2008. Context dependency of litter-mixing effects on decomposition and nutrient release across a long-term chronosequence. *Oikos*, 117: 1674–1682.

Kutbay, H.G. 2000. Sclerophyll in *Franxinus angustifolia* Vahl. subsp. *oxycarpa* (Bieb. ex Willd.) Fanco & Rocha Afonso and *Laurus nobilis* L. and edaphic relations of these species. *Turkish Journal of Botany* 24: 113–119.

Lavelle, P., Blanchart, E., Martin, A., Martin, S., Spain, A., Toutain, F., Barois, I., Schaefer, R. 1993. A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica* 25: 130–150.

Lewis, S.L., López-González, G., Sonké, B, Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo, K.M.-N., Ewango, C. E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.-R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S.-H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R. & Wöll, H. 2009. Increasing carbon storage in intact African tropical forests. *Nature* 457: 1003–1007.

Doi: 10.1111/j.1654-1103.2011.01352.x © 2011 International Association for Vegetation Science

Madritch, M.D. & Cardinale, B.J. 2007. Impacts of tree species diversity on litter decomposition in northern temperate forests of Wisconsin, USA: a multi-site experiment along a latitudinal gradient. *Plant and Soil* 292: 147–159.

McClaughterty, C.A., Pastor, J. & Aber, J.D. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology* 66: 266–275.

Meentemeyer, V. 1984. The geography of organic decomposition rates. *Annals of the Association of American Geographers* 74: 551–560.

Melillo, J.M., Aber, J.D. & Muratore, J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621–626.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44: 322–331.

Pastor, J. & Post, W.M. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2: 3–27.

Peh, K.S.-H., Lewis, S.L. & Lloyd, J. 2011a. Mechanisms of monodominance in diverse tropical tree-dominated systems. *Journal of Ecology* 99: 891–898.

Peh, K.S.-H., Sonké, B., Lloyd, J., Quesada, C.A. & Lewis, S.L. 2011b. Soil does not explain monodominance in a Central African tropical forest. *PLoS ONE*, 6: e16996.

Peñuelas, J. & Estiarte, M. 1997. Trends in plant carbon concentration and plant demand for N throughout this century. *Oecologia* 109: 69–73.

Powers, J.S., Montgomery, R.A., Adair, E.C., Brearley, F.Q., DeWalt, S.J., Castanho, C.T., Chave, J., Deinert, E., Ganzhorn, J.U., Gilbert, M.E., González-Iturbe, J.A., Bunyavejchewin, S., Grau, H.R., Harms, K.E., Hiremath, A., Iriarte-Vivar, S., Manzane, E., de Oliveira, A.A., Poorter, L., Ramanamanjato, J.-B., Salk, C., Varela, A., Weiblen, G.D. & Lerdau, M.T. 2009. Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. *Journal of Ecology* 97: 801–811.

Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.

Rubinstein, A. & Vasconcelos, H.L. 2005. Leaf-litter decomposition in Amazonian forest fragments. *Journal of Tropical Ecology* 21: 699–702.

Scherer-Lorenzen, M., Bonilla, J.L. & Potvin, C. 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. *Oikos* 116: 2108–2124.

Schlesinger, W. H. 1991. *Biogeochemistry*. Academic Press, San Diego, CA, US.

Silver, W.L. & Miya, R.K. 2001. Global patterns in root decomposition: comparisons of climate and litter quality. *Oecologia* 129: 407–419.

Songwe, N.C., Okali, D.U.U. & Fasehun, F.E. 1995. Litter decomposition and release in a tropical rainforest, Southern Bakundu Forest Reserve, Cameroon. *Journal of Tropical Ecology* 11: 333–350.

Swift, M.J., Heal, O.W. & Anderson, J.M. 1979. *Decomposition in terrestrial ecosystems*. University of California Press, Berkeley, CA, US.

Torti, S.D., Coley, P.D. & Kursar, T.A. 2001. Causes and consequences of monodominance in tropical lowland forests. *American Naturalist* 157: 141–153.

Villela, D.M. & Proctor, J. 2002. Leaf litter decomposition and monodominance in the *Peltogyne* forest of Maracá Island, Brazil. *Biotropica* 34: 334–347.

Vitousek, P.M. & Farrington, H. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biochemistry* 37: 63–75.

Wardle, D.A. & Zackrisson, O. 2005. Effects of species and functional group loss on island ecosystem properties. *Nature* 435: 806–810.

Wardle, D.A., Bardgett, R.D., Walker, L.R., Peltzer, D.A. & Lagerstrom, L. 2008. The response of plant diversity to ecosystem retrogression: evidence from contrasting long-term chronosequences. *Oikos* 117: 93–103.

Wieder, R.K. & Wright, S.J. 1995. Tropical forest litter dynamics and dry season irrigation on Barro Colorado Island, Panama. *Ecology* 76: 1971–1979.