



Diversity and ecosystem functioning: Litter decomposition dynamics in the Atlantic Rainforest

Urs Christian Gießelmann^{a,*}, Kelly Geronazzo Martins^b, Martin Brändle^a,
Martin Schädler^c, Renato Marques^b, Roland Brandl^a

^a University of Marburg, Department of Animal Ecology, Karl-von-Frisch-Straße 8, 35032 Marburg, Germany

^b Universidade Federal do Paraná, Departamento de Solos e Engenharia Agrícola, Laboratório de Biogeoquímica, Rua dos Funcionários 1540, 80035050 Curitiba, Brazil

^c Helmholtz-Centre for Environmental Research - UFZ, Department Community Ecology, Theodor-Lieser-Straße 4, 06110 Halle, Germany

ARTICLE INFO

Article history:

Received 15 March 2010

Received in revised form 22 July 2010

Accepted 23 July 2010

Keywords:

Decomposition

Diversity

Atlantic Rainforest

Ecosystem functioning

ABSTRACT

The relationship between ecosystem functioning and species diversity is important for conservation and restoration management of endangered ecosystems. Here we experimentally analysed the effects of tree species richness and composition on the fundamental ecosystem process of leaf litter decomposition in the Brazilian Atlantic Rainforest. We measured the decomposition rates of leaf litter of eight broad-leaved, native tree species either individually or in mixtures of two, four, or six species. Additionally, we analysed the effect of macro- and meso-invertebrate exclusion using coarse- and fine-meshed litter bags. Species composition, but not species richness, significantly influenced litter decomposition rates. Invertebrate exclusion also influenced litter decomposition, although this effect varied between species and mixtures. Overall, litter decomposition dynamics was non-additive, i.e. observed decomposition rates of litter mixtures differed from what would be expected from the decomposition rates of their component species. However, there were also differences between mixtures, which could be at least partly attributed to the varying influence of invertebrates. We conclude that the relationship between the decomposition subsystem and species diversity in the Atlantic Rainforest follows the idiosyncratic response hypothesis and not the rivet hypothesis. For conservation or reforestation management, our results emphasise the need to maintain or restore the composition of locally native tree species communities rather than to maintain only a high tree species richness.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

The relationship between biodiversity and ecosystem processes is of central interest to assess the effect of global change on ecosystem functioning (Hooper et al., 2005; Cardinale et al., 2006; Balvanera et al., 2006). Ecosystem processes may dramatically change as species become extinct, often with unpredictable consequences (Naeem et al., 1994; Tilman, 1999). A great number of species will be lost especially in species-rich tropical rainforests owing to human activity (Dirzo and Raven, 2003; Hansen et al., 2008). Nearly 50% of the tropical closed-canopy forest has already been transformed into farmland, pasture, plantation or secondary forest (Wright, 2005). Hence, the accompanying loss of species may have severe impacts on tropical ecosystem functions, but more experimental investigations are needed.

The recent debate on the importance of biodiversity as a key determinant for ecosystem processes and stability prompted

a flood of experimental and theoretical studies on the underlying mechanisms and patterns (McCann, 2000). The early hypotheses—the rivet hypothesis (Ehrlich and Ehrlich, 1981) and the idiosyncratic response hypothesis (Lawton, 1994)—provide a conceptual basis for the interpretation of observed patterns. Their basic difference lies in the importance placed on species identity and species richness. The rivet hypothesis assumes a certain degree of redundancy between functionally similar species within a community, whereas the idiosyncratic response hypothesis assumes the unpredictability of the relationship between ecosystem functioning and species diversity because of the complex and varied influences of individual species (Mikola and Setälä, 1998). Thus, species richness has a greater relevance in the rivet hypothesis, and species identity has a greater impact in the idiosyncratic response hypothesis. The former hypothesis has been further modified according to the assumed degree of redundancy of species (see redundancy hypothesis, Walker, 1992; and equal importance hypothesis, Vitousek and Hooper, 1993).

An understanding of the relationship between important ecosystem processes and species diversity would provide valuable implications for conservation and restoration management

* Corresponding author. Tel.: +49 6421 2826819; fax: +49 6421 28 23387.

E-mail address: giesselu@staff.uni-marburg.de (U.C. Gießelmann).

Table 1
Plant species used, mixture composition and *k*-values after 6 months.

Species no.	Species	Family	<i>k</i> -Value	
			Fine-meshed litter bag	Coarse-meshed litter bag
1	<i>Alchornea glandulosa</i> (Ag)	Euphorbiaceae	2.13	3.93
2	<i>Alchornea triplinervia</i> (At)	Euphorbiaceae	2.92	4.34
3	<i>Cabrlea canjerana</i> (Cc)	Meliaceae	2.23	3.76
4	<i>Marliera tomentosa</i> (Mt)	Myrtaceae	0.92	0.78
5	<i>Matayba guianensis</i> (Mg)	Sapindaceae	1.44	1.57
6	<i>Pera glabrata</i> (Pg)	Euphorbiaceae	1.12	2.90
7	<i>Inga edulis</i> (Ie)	Fabaceae	1.24	1.35
8	<i>Sloanea guianensis</i> (Sg)	Elaeocarpaceae	1.52	1.89
Mixture no.	Mixture		<i>k</i> -Value	
			Fine-meshed litter bag	Coarse-meshed litter bag
9	Mt, Pg		0.94	1.31
10	Ie, Pg		1.04	1.81
11	Mt, Sg		1.27	1.40
12	At, Mg		1.77	2.60
13	Sg, Pg, Mt, Cc		1.40	2.01
14	Pg, Mg, Cc, At		1.60	2.49
15	Mg, Ag, Sg, At		1.91	2.68
16	At, Mt, Mg, Sg		1.40	1.68
17	Cc, Mt, Sg, Ag, At, Pg		1.68	2.27
18	At, Mt, Ag, Cc, Pg, Ie		1.59	2.35
19	Mg, Pg, Cc, Ag, Mt, Sg		1.62	1.93
20	At, Mt, Sg, Cc, Pg, Mg		1.64	2.24

(Palmer et al., 1997). If the relationship follows the rivet hypothesis, the main focus of restoration would be on the number of species, depending on the degree of redundancy. Which species are present would be of minor interest. If the relationship follows the idiosyncratic response hypothesis, the main focus would be on the actual species used for restoration.

The decomposition of plant litter is an essential process in terrestrial ecosystems, resulting in carbon and nutrients being recycled for primary production (Swift et al., 1979). Given that most of the plant material produced is in this way returned to the ecosystem, the importance of plant species richness and composition for ecosystems may be largely determined by their impact on litter decomposition (Wardle et al., 1997; Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Species richness effects on decomposition dynamics in litter mixtures arise from direct or indirect interactions between component species, independent of their identity, which leads to non-additive decomposition dynamics of litter mixtures (Ball et al., 2008). Compositional effects arise from the interactions or the presence/absence of certain species. Interactions between certain species lead to non-additive decomposition dynamics. If there are no interactions, but species differ in their decomposability, presence/absence of certain species leads to additive decomposition dynamics. In both cases, the identity of the species is important. A pure species richness effect would point to a relationship between diversity and litter decomposition following the rivet hypothesis, whereas a compositional effect would indicate an idiosyncratic relationship.

In previous studies on the effect of species richness and composition of litter mixtures on decomposition rates, non-additive effects of combining different litter types dominated, whereas the species richness of litter assemblages did not seem to be an important driver of decomposition processes (for reviews, see Gartner and Cardon, 2004; Hättenschwiler et al., 2005). The non-additive effects of mixing different litter types on decomposition dynamics are mostly attributed to the activity of the decomposer fauna (Hättenschwiler and Gasser, 2005; Schädler and Brandl, 2005). Thus, an effect of species richness and/or species composition on litter decomposition should be mediated by changes in the activity of soil biota involved in decomposition. A plant-species-rich litter

mixture may support a species-rich invertebrate fauna because of: (i) differences in the attractiveness of certain litter types to different species of invertebrates and (ii) increased microhabitat diversity. Such a complementary use of resources by the decomposers may lead to an increased decomposition rate. Evidence for these effects is, however, scarce, and most studies point to the overwhelming importance of litter type identity and quality rather than the plant species richness of the litter for faunal diversity (Wardle et al., 2006; Zhang et al., 2008).

Litter decomposition is particularly important in the tropics because of the low nutrient storage capacity and the high turnover and uptake of nutrients in tropical soils. Furthermore, invertebrate fauna contribute comparatively more to decomposition in the tropics than in lower or higher latitudes because of the more favourable and stable climatic conditions (Henaghan et al., 1998; Lavelle et al., 1993; Beck, 2000; González and Seastedt, 2001; Wall et al., 2008; Schmidt et al., 2008; Yang and Chen, 2009). Thus, invertebrate fauna may play a much greater role as agents of non-additive litter mixing effects in the tropics.

We investigated the influence of litter species richness, litter mixture composition, and invertebrate activity on litter decomposition in the highly species-diverse Atlantic Rainforest in Brazil. This rainforest is highly endangered: only 11.7% of the original 150 million ha remain (Ribeiro et al., 2009). Of these remnants, 32–40% are small fragments (<50 ha) or less-species-rich secondary forests. This trend of forest destruction, fragmentation and transformation into secondary forests causes a serious loss of biodiversity at the local and regional scales (Laurance, 2007; Barlow et al., 2007; Bihn et al., 2008; Metzger, 2009). Hence, it is important to investigate whether this loss of biodiversity causes a change in ecosystem functioning, e.g. in litter decomposition and consequently in nutrient and carbon cycling. In this context, we investigated whether litter decomposition is affected by species richness or species composition of the litter or both. Because these effects might be largely attributed to the soil biota involved in the decomposition, we also examined the effect of invertebrate exclusion. Our results allow us to draw conclusions on the relationship between the decomposition subsystem and plant species diversity in the Atlantic Rainforest.

2. Materials and methods

2.1. Study site

As a part of the MATA ATLANTICA Project, a German–Brazilian cooperation, this study was initiated in the Atlantic Rainforest in the Brazilian state of Paraná, in the Cachoeira nature reserve (25.25°S, 48.68°W, 147 NN). The study area consists of secondary rainforest sites of different successional age (5 to >100 years) after usage as pasture. A forest site of medium successional age (35–50 years) was chosen for our experiment as it provides sufficient tree species on a small local scale and represents an achievable aim for reforestation.

2.2. Experimental set-up

The eight most abundant broad-leaved tree species on the study site were chosen for the experiment (Table 1). Mature leaves were sampled directly from trees in July/August 2007. Leaves were air-dried, and a sub-sample of each type was oven-dried to determine dry weight. Air-dried leaves (4 ± 0.1 g) of each tree species were placed in litter bags (25 cm \times 25 cm). In addition, air-dried leaves of two randomly chosen species (2 ± 0.08 g each; four different mixtures), four randomly chosen species (1 ± 0.06 g each; four different mixtures), and six randomly chosen species (0.66 ± 0.04 g each; four different mixtures) were placed in litter bags (Table 1). In this way, component species as well as species composition were replicated, and effects of species composition and of species richness could be separated (Schmid et al., 2002). Each litter bag set-up was replicated 20 times. The nylon litter bags used for half of the replicates were of a coarse mesh size (5 mm \times 5 mm) to allow passage of soil macro- and meso-invertebrates. The other nylon litter bags were of a fine mesh size (20 μ m \times 20 μ m) to exclude macro- and meso-fauna, but to allow access by bacteria, fungal hyphae, nematodes and protozoa. We are aware, that litter bags, especially fine-meshed bags, have the potential to alter the microclimate within the bags by influencing moisture and temperature (Bradford et al., 2002). As this effect is greater for fine-meshed bags, differences between decomposition rates within fine and coarse-meshed bags might be due to microclimatic differences rather than invertebrate exclusion. Nevertheless, due to the favourable and stable climatic conditions on our study site, microclimatic differences should be less important than invertebrate exclusion.

In August 2007, the litter bags were placed in five blocks (about five meters apart) using a randomised block design (two replicates per mesh size within each block). The forest floor was cleared of litter cover to avoid an artificial increase in litter diversity. Litter bags were placed on the bare soil and secured with wire hooks. Half of the litter bags were collected after 3 months, and the other half after 6 months. Thus, the total number of litter bags was 400 with 20 mixtures (including single species) \times 2 mesh sizes \times 5 blocks \times 2 sampling dates. The leaf material remaining in the bags was oven-dried, cleaned (by carefully removing adhesive dirt with a paintbrush) and weighed. The remaining leaf mass of all samples was incinerated at approx. 600 °C to obtain ash-free dry weight to account for inorganic contamination. The decomposition rate was defined as the percent dry-weight loss.

As a measure for decomposability we calculated *k*-values after 6 months of decomposition according to Olson (1963) for each of the litter types.

2.3. Data analysis

The percent dry-weight loss was arcsine square-root transformed prior to all statistical analyses to approximate the normal distribution of residuals and to reduce variance heterogeneity. A nested general linear model (GLM) type III sum of squares was used to test the effects on decomposition rates of species richness,

species composition (leaves of single species and mixtures; nested in richness), invertebrate exclusion, and time. Blocks were considered as a random factor in the analysis. The effect of invertebrate exclusion for each species and mixture was additionally tested by ANOVA.

Another approach was used to examine additive and non-additive effects of species loss following the method suggested by Ball et al. (2008). For this, a GLM (type I) sum of squares with litter disappearance as the dependent variable was used. We sequentially included time, block and the presence/absence of each single species as factors in the model. Time had two levels, and block had five levels. The species presence/absence terms had two levels each. As we used type I sum of squares, the order in which the presence/absence terms were included was important. We calculated omega square effect size from a GLM with type III sum of squares with percentage dry-weight loss as dependent variable and all single species as independent variables and included them into the former model in ascending order. We also included the interactions between presence/absence terms and time. Then we included a species interaction term with 20 levels, each representing one of the litter mixtures. A significant species interaction term would indicate non-additivity owing to species richness and/or composition of litter mixtures. Next, we included a species richness term with four levels (1, 2, 4, and 6 species) instead of the species interaction term to explore whether species richness is responsible for non-additive effects. If the richness term was significant, we again included the species interaction term representing the effect of composition into the model and retained the richness term. Significance of both terms would indicate the co-occurrence of non-additive richness and composition effects. Additionally we included an invertebrate exclusion term (two levels) to test whether additive or non-additive effects could be attributed to the activity of the decomposer fauna. We dealt with this term as with the richness term above.

To explore whether additivity or non-additivity was consistent throughout the mixtures, we used the method of Wardle et al. (1997) and investigated whether the decomposition rates of each leaf litter mixture can be predicted from the decomposition rates of individual leaf litter types. For this, the expected amount of dry weight remaining in leaf mixtures (R_e) was calculated by using the observed mass loss of individual leaf litter types, assuming no diversity effects. We used the formula: $[R_e = \sum m_i \times p_{mi}]$, with m_i = initial mass of leaves of species *i* in the mixture and p_{mi} = decomposition rate of leaves of species *i* without leaves of other species (Schädler and Brandl, 2005). This equation takes into account differences in initial leaf masses of component species. The observed litter masses remaining in mixtures (R_o) in relation to expected values were calculated as $[100 \times (R_o - R_e)/R_e]$ per block. Deviations from zero indicate non-additive effects of litter mixing and were tested using 95% confidence intervals. Additionally, another GLM (type III sum of squares) was used to test the influence of species richness, species composition (nested in richness), invertebrate exclusion and time on the deviation of the remaining litter mass from the expected litter mass (see first analysis). Furthermore, we used an approach similar to that of Wardle et al. (1997) to investigate whether non-additive effects were generated by the presence/absence of invertebrates. For this, we calculated the expected influence of macroinvertebrates on the decomposition of leaf litter mixtures using the observed invertebrate effect on the component litter type when decomposing alone. This effect was defined as the difference between remaining proportions of litter dry weight in fine- and coarse-meshed bags containing one leaf litter type. The expected remaining litter mass of mixtures in course-meshed bags (R_{ec}) was calculated as $[R_{ec} = R_{of} + \sum m_i e_i]$, with R_{of} = observed remaining litter mass of mixture *j* in fine-meshed bags, e_i = effect of invertebrates on decomposition of litter of species *i*, and m_i = initial mass of component species *i*. Again we

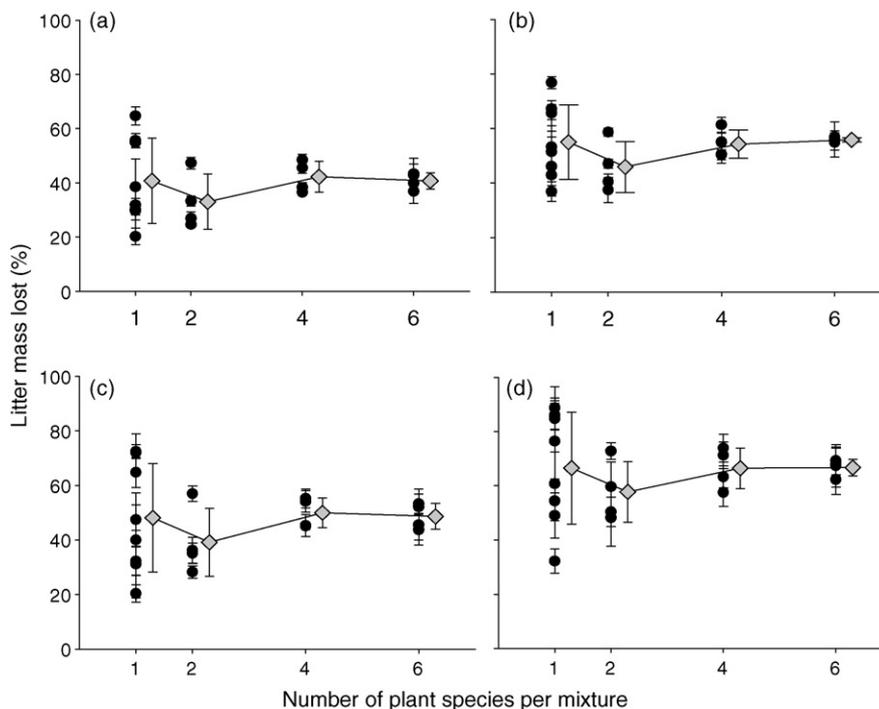


Fig. 1. Percentage of the initial leaf litter mass lost for all tree species and mixtures (black circles; mean \pm standard error, five replicates) and richness levels (grey diamonds; mean \pm standard error, with species and mixtures as replicates), eight replicates for single species and four replicates for mixtures (a) after 3 months from fine-meshed bags, (b) after 6 months from fine-meshed bags, (c) after 3 months from coarse-meshed bags and (d) after 6 months from coarse-meshed bags.

calculated the observed litter masses remaining in coarse-meshed bags (Ro_c) in relation to expected values as $[100 \times (Ro_c - Re_c)/Re_c]$ per block and tested for significant deviations from zero as an indication of non-additivity using 95% confidence intervals. All analyses were done using Statistica, version 6. For more information on the statistical procedures see Supplementary Table S1.

3. Results

We found a great variation in k -values of the different litter types when decomposing alone in the presence (0.78–4.34) and absence (0.92–2.92) of invertebrates (Table 1).

The amount of remaining litter mass was insufficient for a quantitative assessment of faunal activity during the decomposition process. However, in several cases we found diplopods and isopods which are important decomposers in our study region (Schmidt et al., 2008) within coarse-meshed litter bags. In contrast, within fine-meshed bags we did not find macro- or meso-invertebrates in any case (Gießelmann, Pers. Obs.). Thus, differences in decomposition rates between coarse- and fine-meshed bags could be attributed to the exclusion of macro- and meso-invertebrates.

The decomposition rates of leaf litter in our experiments were not influenced by the species richness of the mixtures (Table 2). In contrast, we found a significant effect of litter composition. These effects were consistent over the 6 months of decomposition as neither the number of species nor the species composition interacted with time (Table 2). We also found a decrease in the variability of litter decomposition across litter assemblages with increasing species richness (Fig. 1). The GLM to test for additivity and non-additivity revealed that all except one (*Sloanea guianensis*) of the litter types used significantly influenced decay dynamics (Table 3). This was consistent over time for all species (no significant interactions). Furthermore, the species interaction term had a significant influence on litter decomposition (Table 3). When the interaction term was replaced with the richness term, the richness term had no influence on litter decomposition ($P = 0.064$). The observed and predicted val-

ues of the remaining litter mass of half of the mixtures significantly deviated in at least one case, which indicated non-additive effects (Fig. 2). These deviations could not be explained by any of the main factors. However, the species composition interacted significantly with time and invertebrate exclusion (Table 4).

In general, the exclusion of invertebrates considerably decreased the litter decomposition rate. However, this effect varied between litter type and mixtures (significant interaction; Table 2). After 3 months as well as after 6 months, the decomposition of the litter of half of the individual leaf types as well as of the litter of mixture 11 did not significantly differ in the presence and absence of invertebrates. Mixture 9 also showed no significant effect of invertebrate exclusion but only after 6 months (Fig. 3). The invertebrate exclusion treatment also interacted with time,

Table 2

The effects of presence/absence of macroinvertebrates, tree species richness of the litter, mixture composition, and decomposition time on the decomposition rate of litter. The effects were tested using a nested GLM with type III sum of squares.

Source	Decomposition rates			
	df	MS	F	P
Constant	1	228.05	677.19	<0.001
Fauna [F]	1	0.90	32.74	<0.001
Species richness ^A [S]	3	0.18	0.55	0.653
Mixture(species richness) ^B [M]	16	0.33	12.09	<0.001
Time [T]	1	2.47	635.49	<0.001
F \times S ^B	3	0.00	0.03	0.989
F \times M(S) ^B	16	0.03	6.94	<0.001
T \times F	1	0.04	14.29	<0.001
S \times T ^C	3	0.01	1.40	0.278
M(S) \times T ^C	16	0.00	0.97	0.521
F \times S \times T ^D	3	0.00	0.20	0.893
F \times M(S) \times T ^D	16	0.00	1.01	0.441
Block	4	0.01	2.31	0.06
Residual	307	0.00		

Each term indicated by an upper case letter was tested against the term with the same letter in lower case; all other terms were tested against the residual. The factor M includes leaf litter mixtures as well as leaf litter of single tree species.

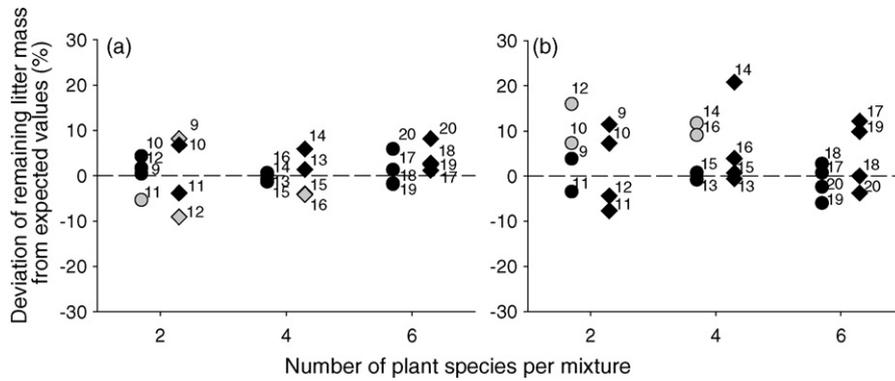


Fig. 2. Percent deviation of observed litter mass remaining from expected values calculated from the leaf litter of one species decomposing alone, in the presence (diamonds) and absence (circles) of macroinvertebrates after (a) 3 months and (b) 6 months. Grey symbols indicate significant deviation from zero (95% confidence interval). Each symbol refers to the mean of a mixture over all blocks (five replicates). Numbers indicate the mixtures (see Table 1). Positive deviations indicate antagonistic effects (i.e. decreased decomposition rates) and negative deviations indicate synergistic effects (i.e. increased decomposition rates).

which suggested a change in the contribution of invertebrates with ongoing decomposition (Table 2). In the test for additivity and non-additivity, invertebrate exclusion as well as its interaction with time showed a significant influence (Table 3). Furthermore, invertebrate presence/absence interaction with species composition had a significant influence on the deviation of observed and expected decomposition rates (Table 4). However, significant deviations from expected values in the presence of invertebrates occurred only after 3 months (Fig. 2). After 6 months, all significant deviations occurred in the absence of invertebrates, though some mixtures including invertebrates also strongly deviated from zero without being significant (Fig. 2). These findings were supported by a comparison of the observed and expected influence of invertebrates. The same mixtures that showed significant deviations

from expected decomposition rates (Fig. 2) showed non-additivity regarding invertebrate influence after 3 months. However, after 6 months, only mixture 12 showed a highly significant non-additive effect in the presence of invertebrates (Fig. 4).

4. Discussion

Our study adds to the growing body of studies that do not report a direct relationship between species richness of leaf litter types and the decomposition rate (Hättenschwiler et al., 2005; Schindler and Gessner, 2009). Unlike the number of leaf litter types, leaf litter identity and mixture composition had a striking influence on litter decomposition (Table 2). The importance of the species identity of the leaf litter and therefore the low degree of functional redundancy

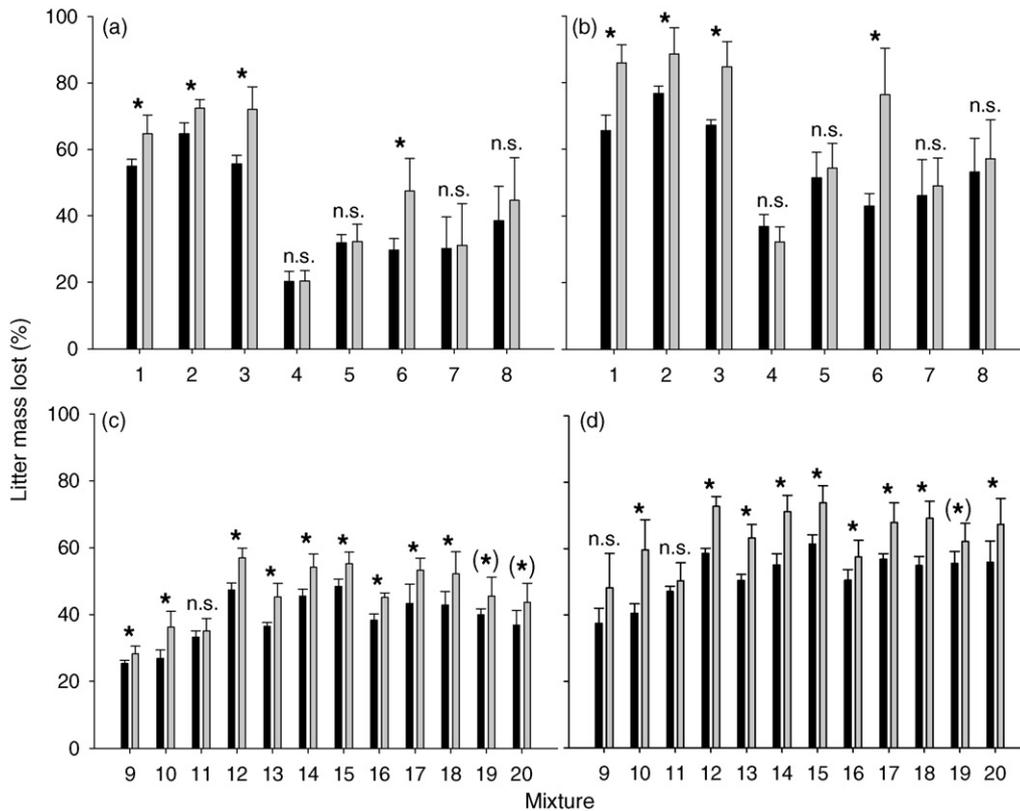


Fig. 3. Percentage of the initial leaf litter mass lost in the presence (grey bars) and absence (black bars) of macroinvertebrates for single species after (a) 3 months and (b) 6 months and for mixtures after (c) 3 months and (d) 6 months, averaged over blocks; error bars are standard deviation. Asterisks indicate significant differences. Numbers indicate the mixtures (see Table 1).

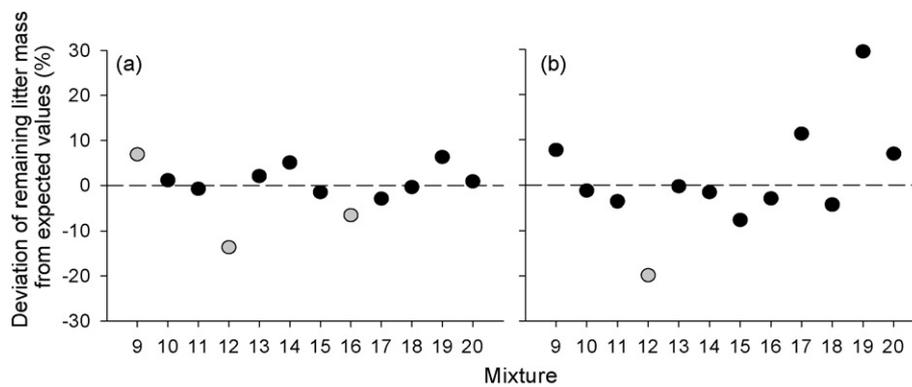


Fig. 4. Percent deviation of observed litter mass remaining from expected values. The deviation was calculated from the influence of macroinvertebrates on the decomposition of the leaf litter of one species for all mixtures after (a) 3 months and (b) 6 months, averaged over blocks. Grey symbols indicate significant deviation from zero (95% confidence interval). Positive deviations indicate antagonistic effects (i.e. observed decomposition rates decreased compared to expected decomposition rates) and negative effects indicate synergistic effects (i.e. observed decomposition rates increased compared to expected). Numbers indicate the mixtures (see Table 1).

was further confirmed by the significant influence of the presence of all but one species on the decomposition rate in leaf litter mixtures (Table 3). However, the significant non-additive effects in our results indicate that differences in litter decomposition cannot be explained exclusively by differences in litter decomposability, but can be explained also by interactions between certain leaf litter types within mixtures. These interactions lead to unpredictable decomposition dynamics. As expected, our test for additivity or non-additivity following the approach of Ball et al. (2008) showed that the non-additive effects observed were due to species composition rather than species richness (Table 3) (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Ball et al., 2008).

In accordance with several other studies, our results demonstrate the importance of invertebrates for decomposition in a tropical rainforest (Beck, 2000; González and Seastedt, 2001; Wall et al., 2008; Yang and Chen, 2009), although this effect could have been overestimated because of microclimatic differences between fine and coarse-meshed bags. Additionally, differences in litter mass loss between fine and coarse-meshed bags could be due to an increased loss of fragmented litter material from coarse-meshed

bags. However, fragmentation of leaves is part of the litter degradation process and mainly performed by larger invertebrates (Swift et al., 1979; Coleman et al., 2004). Therefore, we agree with Bradford et al. (2002) and consider the breakdown and loss of small litter fragments from the sample as a functional role of decomposing invertebrates. However, the effect of invertebrates on decomposition varied considerably among leaf litter types and mixtures (Fig. 3). This variation is probably caused by differences in litter chemistry and consequently palatability of the different litter types for invertebrates (Seastedt, 1984; Loranger, 2002; Schädler et al., 2003). We further showed that the non-additive effects of litter mixing were largely attributable to the activity of invertebrates involved in decomposition (Table 3; Fig. 2). Therefore, the varying effect of invertebrates on the decomposition of various types of leaf litter may also account for differences in non-additivity between mixtures. For example, the decomposition rate of mixture 9 in the presence of invertebrates was significantly lower than expected values after 3 months and was even lower after 6 months, even if not significant. This mixture includes leaves of *Marlieara tomentosa*, which decompose slowly when not mixed with leaves of other tree species, irrespective of the presence or absence of invertebrates (Fig. 3). By contrast, leaves of *Pera glabrata*, the other species in the mixture, decompose rapidly in the presence of invertebrates. The genus *Marlieara* belongs to the family Myrtaceae. Members

Table 3

Additive and non-additive effects of leaf litter mixing on leaf litter decomposition. The effects were tested using a GLM with type I sum of squares.

Source	Decomposition rates			
	df	MS	F	P
Time	1	2.60	523.26	<0.001
Block	4	0.01	1.25	0.291
<i>Sloanea guianensis</i>	1	0.01	1.92	0.166
<i>Pera glabrata</i>	1	0.12	24.67	<0.001
<i>Alchornea glandulosa</i>	1	0.85	170.68	<0.001
<i>Matayba guianensis</i>	1	0.05	9.16	<0.001
<i>Inga edulis</i>	1	0.42	85.18	<0.001
<i>Cabralea canjerana</i>	1	0.80	160.31	<0.001
<i>Alchornea triplinervia</i>	1	0.74	149.38	<0.001
<i>Marlieara tomentosa</i>	1	1.47	295.12	<0.001
Species interaction term	11	0.12	24.66	<0.001
Fauna	1	1.00	201.24	<0.001
Time × <i>Sloanea guianensis</i>	1	0.0014	0.27	0.602
Time × <i>Pera glabrata</i>	1	0.0086	1.73	0.189
Time × <i>Alchornea glandulosa</i>	1	0.0012	0.24	0.625
Time × <i>Matayba guianensis</i>	1	0.0019	0.38	0.535
Time × <i>Inga edulis</i>	1	0.0017	0.34	0.562
Time × <i>Cabralea canjerana</i>	1	0.0185	3.72	0.054
Time × <i>Alchornea triplinervia</i>	1	0.0001	0.03	0.867
Time × <i>Marlieara tomentosa</i>	1	0.0000	0.01	0.929
Time × Species interaction term	11	0.0040	0.81	0.632
Time × Fauna	1	0.07	13.50	<0.001
Residual	345	0.01		

Table 4

The deviation of the remaining leaf litter mass from expected values. The effects of presence/absence of macroinvertebrates, tree species richness of the litter, mixture composition, and decomposition time were tested using a nested GLM with type III sum of squares.

Source	Deviation from expected values			
	df	MS	F	P
Constant	1	967.30	1.55	0.249
Fauna [F]	1	7.50	0.03	0.866
Species richness ^A [S]	2	11.17	0.03	0.971
Mixture(species richness) ^B [M]	9	379.57	0.98	0.492
Time [T]	1	471.49	2.76	0.131
F × S ^B	2	149.96	0.60	0.569
F × M(S) ^B	9	249.95	7.11	0.004
T × F	1	0.08	0.00	0.964
S × T ^C	2	164.47	0.96	0.418
M(S) × T ^C	9	171.02	4.86	0.014
F × S × T ^D	2	79.98	2.27	0.159
F × M(S) × T ^D	9	35.19	0.33	0.966
Block	4	358.38	3.31	0.012
Residual	182	108.32		

Each term indicated by an upper case letter was tested against the term with the same letter in lower case; all other terms were tested against the residual. The factor M includes leaf litter mixtures as well as leaf litter of single tree species.

of this family contain many polyphenols and essential oils, which can be expected to prevent invertebrate feeding (Rosenthal and Berenbaum, 1991; Hättenschwiler and Vitousek, 2000). Thus, it seems likely that antagonistic effects of this mixture are due to the influence of *M. tomentosa* on invertebrate decomposers. As another example, mixture 12 consists of easily decomposable (*Alchornea triplinervia*) and poorly decomposable (*Matayba guianensis*) leaves; this mixture showed a significant synergistic effect after 3 months in the presence of invertebrates and a significant antagonistic effect in the absence of invertebrates after 6 months. A rather similar pattern was found for mixture 16, which contained leaves of three species with low decomposability (*M. tomentosa*, *M. guianensis*, *S. guianensis*) and leaves of one species with high decomposability (*A. triplinervia*). The non-additive effects of these examples were due to the influence of invertebrates, as confirmed by these mixtures also having congruent significant deviations between the observed and expected invertebrate effect (Fig. 4). However, the influence of invertebrates on non-additivity is restricted to the earlier decomposition phase. In the later phase, significant non-additive effects occurred solely in the absence of invertebrates. Thus, other members of the decomposer community, such as micro-invertebrates or fungi, must be responsible for these non-additive effects. As an exception, mixture 12 showed a significant negative deviation from the expected invertebrate effect after 6 months. However, there was no significant deviation between the observed and expected overall decomposition values in the presence of invertebrates but significant positive deviations in the absence of invertebrates. Thus, the synergistic non-additivity caused by invertebrates seemed to be masked by antagonistic non-additive effects caused by other members of the decomposer community, leading to “pseudo-additivity” (Schindler and Gessner, 2009). This exception suggests that a lack of deviation between observed and expected decomposition values do not ultimately rule out non-additive effects. Additionally, we found relatively strong but non-significant deviations between observed and expected decomposition values for some mixtures in the presence of invertebrates after 6 months (Fig. 2). The fact, that they were not significant might be attributed to a high variability in the invertebrate effect among blocks. This points to a patchy distribution of invertebrates on our study site. Thus, the effect of invertebrates on decomposition also varies spatially. The findings presented highlight the high degree of idiosyncrasy of decomposition dynamics in our study owing to species identity and specific interactions enhanced by invertebrate decomposer activity (see also Chapman et al., 1988; Blair, 1990; Wardle et al., 1997; Bardgett and Shine, 1999).

Although we found no direct effect of species richness on decomposition, the number of tree species might nevertheless influence the decomposition process in other ways. In accordance with other studies (Schädler and Brandl, 2005; Lecerf et al., 2007; Keith et al., 2008), we found a decreasing variability in decomposition rates with increasing tree species richness of the litter (Fig. 1). Lecerf et al. (2007) and Keith et al. (2008) interpret such a reduction of variability in the decomposition rate as a component of higher ecosystem stability concerning ecosystem processes (e.g. decomposition). Following the “variance reduction effect” postulated by Huston (1997), this reduction is just due to the increasing similarity of mixtures drawn from a limited species pool. Studies of larger species pools are necessary to evaluate whether there might be a stabilizing effect of litter diversity on the decomposition rate across litter mixtures with a limited overlap in species composition.

5. Conclusions

The differences in decomposition rate of the leaf litter, the significant influence of the presence/absence of almost all single species

on the decomposition and the specific interactions between certain species, which leads to unpredictable non-additive effects in some cases, highlight the importance of leaf litter identity and the low degree of redundancy of leaf litter type in our experiment. This, combined with the specific and varying effect of macroinvertebrates, involved in the decomposition points to a relationship between the decomposer subsystem and plant species diversity in the Atlantic Rainforest following the idiosyncratic response hypothesis.

For conservation or reforestation management, our results accentuate the need to keep or restore the composition of locally native tree species communities rather than to maintain only a high tree species richness. Our study complements theoretically the practical reforestation experiences that were made during the last 30 years in the Brazilian Atlantic Forest (for a review, see Rodrigues et al., 2009).

Acknowledgements

This study was supported by the German Federal Ministry of Education and Research (BMBF; SOLOBIOMA Project 01LB0201) and the Brazilian National Council for Scientific and Technological Development (CNPq; Proc. 590042/2006-8) within the Brazilian–German Mata Atlântica program. The Brazilian NGO Society for Wildlife Research and Environmental Education (SPVS) permitted and supported the fieldwork at their reserve “Reserva Natural Rio Cachoeira”. The lab work was carried out at the Federal University of Parana (UFPR). We thank Karen A. Brune for proof reading and two anonymous reviewers for commenting on earlier versions of this manuscript.

Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.apsoil.2010.07.006.

References

- Ball, B.A., Hunter, M.D., Kominoski, J.S., Swan, C.M., Bradford, M.A., 2008. Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. *J. Ecol.* 96, 303–313.
- Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Espósito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., Peres, C.A., 2007. Quantifying the biodiversity value of tropical primary, secondary and plantation forests. *Proc. Natl. Acad. Sci. U.S.A.* 104, 18555–18560.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156.
- Bardgett, R.D., Shine, A., 1999. Linkages between plant species diversity, soil microbial biomass and ecosystem function in temperate grasslands. *Soil Biol. Biochem.* 31, 317–321.
- Beck, L., 2000. Streuabbau und Bodenfauna in Wäldern gemäßigter und tropischer Breiten. *Carolinea* 58, 243–256.
- Bihn, J.H., Verhaagh, M., Braendle, M., Brand, R., 2008. Do secondary forests act as refuges for old growth forest animals? Recovery of ant diversity in the Atlantic forest of Brazil. *Biol. Conserv.* 141, 733–743.
- Blair, J.M., 1990. Decay rates, nitrogen fluxes and decomposer communities in single and mixed species foliar litter. *Ecology* 71, 1976–1985.
- Bradford, M.A., Tordoff, G.M., Eggers, T., Jones, T.H., Newington, J.E., 2002. Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos* 99, 317–323.
- Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443, 989–992.
- Chapman, K., Whittaker, J.B., Heal, O.W., 1988. Metabolic and faunal activity in litters of tree mixtures compared with pure stands. *Agric. Ecosyst. Environ.* 24, 33–40.
- Coleman, D.C., Crossley Jr., D.A., Hendrix, P.F., 2004. *Fundamentals of Soil Ecology*, second ed. Elsevier Academic Press.
- Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. *Annu. Rev. Environ. Resour.* 28, 137–167.
- Ehrlich, P.R., Ehrlich, A.H., 1981. *Extinction: The Causes and Consequences of the Disappearance of Species*. Random House, New York.

- Gartner, T.B., Cardon, Z.B., 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos* 104, 230–246.
- González, G., Seastedt, T.R., 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* 82, 955–964.
- Hansen, M.C., Stehman, S.V., Potapov, P.V., Loveland, T.R., Townshend, J.R.G., DeFries, R.S., Pittman, K.W., Arunawati, B., Stolle, F., Steininger, M.K., Carroll, M., DiMiceli, C., 2008. Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. *Proc. Natl. Acad. Sci. U.S.A.* 105, 9439–9444.
- Hättenschwiler, S., Vitousek, P.M., 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. *Tree* 15, 238–243.
- Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 36, 191–218.
- Hättenschwiler, S., Gasser, P., 2005. Soil animals alter plant litter diversity effects on decomposition. *Proc. Natl. Acad. Sci. U.S.A.* 102, 1519–1524.
- Henaghan, L., Coleman, D.C., Zou, X., Crossley Jr., D.A., Haines, B.L., 1998. Soil microarthropods community structure and litter decomposition dynamics: a study of tropical and temperate sites. *Appl. Soil Ecol.* 9, 33–38.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75, 3–35.
- Huston, M.A., 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110, 449–460.
- Keith, A.M., van der Wal, R., Brooker, R.W., Osler, G.H.R., Chapman, S.J., Burslem, D.F.R.P., Elston, D.A., 2008. Increasing litter species richness reduces variability in a terrestrial decomposer system. *Ecology* 89, 2657–2664.
- Laurance, W.F., 2007. Have we overstated the tropical biodiversity crisis? *Tree* 22, 65–70.
- Lavelle, P., Blanchart, E., Martin, A., Martin, S., Spain, A., 1993. A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica* 25, 130–150.
- Lawton, J.H., 1994. What do species do in ecosystems? *Oikos* 71, 367–374.
- Lecerf, A., Risnoveanu, G., Popescu, C., Gessner, M.O., Chauvet, E., 2007. Decomposition of diverse litter mixtures in streams. *Ecology* 88, 219–227.
- Loranger, G., 2002. Leaf decomposition in two semi-evergreen tropical forests: influence of litter quality. *Biol. Fertil. Soils* 35, 247–252.
- McCann, K.S., 2000. The diversity–stability debate. *Nature* 405, 228–233.
- Metzger, J.P., 2009. Conservation issues in the Brazilian Atlantic forest. *Biol. Conserv.* 142, 1138–1140.
- Mikola, J., Setälä, H., 1998. Relating species diversity to ecosystem functioning: mechanistic backgrounds and experimental approach with a decomposer food web. *Oikos* 83, 180–194.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., Woodfin, R.M., 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368, 734–737.
- Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44, 322–331.
- Palmer, M.A., Ambrose, R.F., LeRoy Poff, N., 1997. Ecological theory and community restoration ecology. *Restor. Ecol.* 5, 291–300.
- Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biol. Conserv.* 142, 1141–1153.
- Rodrigues, R.R., Lima, R.A.F., Gandolfi, S., Nave, A.G., 2009. On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biol. Conserv.* 142, 1242–1251.
- Rosenthal, G.A., Berenbaum, M.R., 1991. *Herbivores: Their Interactions with Secondary Plant Metabolites*. Academic Press, New York.
- Schädler, M., Jung, G., Auge, H., Brandl, R., 2003. Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. *Oikos* 103, 121–132.
- Schädler, M., Brandl, R., 2005. Do invertebrate decomposers affect the disappearance rate of litter mixtures? *Soil Biol. Biochem.* 37, 329–337.
- Schindler, M.H., Gessner, M.O., 2009. Functional leaf traits and biodiversity effects on litter decomposition in a stream. *Ecology* 90, 1641–1649.
- Schmid, B., Hector, A., Huston, M.A., Inchausti, P., Nijs, I., Leadley, P.W., Tilman, D., 2002. The design and analysis of biodiversity experiments. In: Loreau, M., Naeem, S., Inchausti, P. (Eds.), *Biodiversity and Ecosystem Functioning. Syntheses and Perspectives*. Oxford University Press, Oxford, pp. 61–75.
- Schmidt, P., Dickow, K., Rocha, A.A., Marques, R., Scheuermann, L., Römbke, J., Förster, B., Höfer, H., 2008. Soil macrofauna and decomposition rates in southern Brazilian Atlantic rainforests. *Ecotropica* 14, 89–100.
- Seastedt, T.R., 1984. The role of microarthropods in decomposition and mineralization processes. *Annu. Rev. Entomol.* 29, 25–46.
- Swift, M., Heal, O.W., Anderson, J.M., 1979. *Decomposition in Terrestrial Systems*. Blackwell Science, Oxford.
- Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80, 1455–1474.
- Vitousek, P.M., Hooper, D.U., 1993. Biological diversity and terrestrial ecosystem biogeochemistry. In: Schulze, E.D., Mooney, H.A. (Eds.), *Biodiversity and Ecosystem Function*. Springer, Berlin, pp. 3–14.
- Wall, D.H., Bradford, M.A., John, M.G.St., Trofymow, J.A., Behan-Pelletier, V., Bignell, D.E., Dangerfield, M., Parton, W.J., Rusek, J., Voigt, W., Wolters, V., Gardel, H.Z., Ayuke, F., Bashford, R., Beljakova, O.I., Bohlen, P.J., Brauman, A., Flemming, S., Henschel, J.R., Johnson, D.L., Jones, T.H., Kovarova, M., Kranabetter, J.M., Kutny, L., Lin, K.-C., Maryati, M., Masse, D., Pokarzhevskii, A., Rahman, H., Sabrá, M.G., Salamon, J.-A., Swift, M.J., Varela, A., Vasconcelos, H.L., White, D., Zou, X., 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Glob. Change Biol.* 14, 1–17.
- Walker, B.H., 1992. Biodiversity and ecological redundancy. *Conserv. Biol.* 6, 18–23.
- Wardle, D.A., Bonner, K.I., Nicholson, K.S., 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* 79, 247–258.
- Wardle, D.A., Yeates, G.W., Barker, G.M., Bonner, K.I., 2006. The influence of plant litter diversity on decomposer abundance and diversity. *Soil Biol. Biochem.* 38, 1052–1062.
- Wright, S.J., 2005. Tropical forests in a changing environment. *Tree* 20, 553–560.
- Yang, X., Chen, J., 2009. Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China. *Soil Biol. Biochem.* 41, 910–918.
- Zhang, P., Tian, X., He, X., Song, F., Ren, L., Jiang, P., 2008. Effect of litter quality on its decomposition in broadleaf and coniferous forest. *Eur. J. Soil Biol.* 44, 392–399.