The use of plant litter and soil fauna traits in a mechanistic assessment of litter decomposition under global change

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Chapter V

Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient

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Abstract

Plant litter decomposition is a key process in terrestrial carbon cycling, yet the relative importance of various control factors remains ambiguous at a global scale. A full reciprocal litter transplant study with 16 litter species that varied widely in traits and originated from four forest sites covering a large latitudinal gradient (subarctic to tropics) showed a consistent interspecific ranking of decomposition rates. At a global scale, variation in decomposition was driven by a small subset of litter traits (water saturation capacity and concentrations of magnesium and condensed tannins). These consistent findings, that were largely independent of the varying local decomposer communities, suggest that decomposer communities show little specialization and high metabolic flexibility in processing plant litter, irrespective of litter origin. Our results provide strong support for using trait-based approaches in modelling the global decomposition component of biosphere-atmosphere carbon fluxes.

Introduction

Plant litter decomposition is one of the cogs in the gear of ecosystem functioning. The decomposition process allows recycling of carbon and nutrients from dead organic matter, fuelling new primary production (Swift *et al.* 1979). Simultaneously, it releases CO_2 back to the atmosphere and thus controls the carbon fluxes between the biosphere and atmosphere (Cadish & Giller 1997; Cornwell *et al.* 2008). It is important to find general mechanisms underlying the decomposition process to improve the predictions of biologically driven global-scale carbon and nutrient fluxes under future climate change scenarios (Chapin *et al.* 2009; Currie *et al.* 2009; Brovkin *et al.* 2012). As decomposition is under the simultaneous control of various factors, determining common drivers of litter decomposition is challenging but essential. A globally applicable predictive framework may appear elusive because plant-produced litter and decomposers interact locally and may co-evolve, resulting in ecosystem- or biome-specific control factors. Here we explored the extent of biome-specific biological control over decomposition using a large reciprocal transplant litter decomposition study across biomes with leaf litter from 16 woody species and varying complexity of decomposer communities.

Litter decomposition is determined by the interaction between resource (plant litter) quality and consumer organisms (decomposers), which are both controlled by the environment (climatic and soil conditions). At the global scale, the environment, and climate in particular, is considered the most important controlling factor of these three components (Berg *et al.* 1993; Aerts 1997; Cadish & Giller 1997; Wall *et al.* 2008; Zhou *et al.* 2008; Powers *et al.* 2009). Global leaf litter decomposition studies traditionally focused on climatic effects that are now reasonably well understood. However, two recent meta-analyses have shown that resource quality or local interspecific variation of leaf litter quality has stronger effects on litter decomposition than climate parameters (Cornwell *et al.* 2008; Zhang *et al.* 2008). These results suggest that resource quality effects may have been underestimated in previous global or large spatial scale litter decomposition studies (Berg *et al.* 1993; Wall *et al.* 2008; Zhou *et al.* 2008; Powers *et al.* 2009), possibly due to a limited number (one or two) of plant litter species included in those studies.

Variation in resource quality can be captured by litter species identity, which includes all characteristics of a species, or by specific litter chemical and physical traits across different species. The global effect of resource quality and its dependence on climate is best examined in

multi-species litter transplant studies with an identical range of resource quality across incubation sites, thus excluding site-specific environment-trait combinations. Two previous studies have used this approach including six to ten litter species (Trofymow *et al.* 2002; Currie *et al.* 2009). Both of these studies tested a range of conventional litter chemical traits and found that the lignin/N ratio was the best proxy for resource quality effects on decomposition. However, it was not reported whether the relative importance of different chemical traits for decomposition was consistent across the gradient, and the chosen litter species did not represent the biomes covered by the transect. Disconnecting the site of origin and site of decomposition of litter species may be problematic because litter identity effects on decomposition can depend on the incubation site (Currie *et al.* 2009; Powers *et al.* 2009). These site-dependent responses have been interpreted as decomposers favouring locally-grown litter species over foreign litter due to long-term adaptation to a particular site-specific litter quality (Hunt *et al.* 1988; Gholz *et al.* 2000; Zhou *et al.* 2008).

To our knowledge, no global litter transplant study has been fully reciprocal, i.e. exposing litter from all site-specific species at all sites. Moreover, none of the previous global litter transplant experiments has specifically included the relative effects of macro-decomposers (e.g. isopods, millipedes, earthworms and termites) in their assessments. This omission may have led to significant underestimates of the actual site-specific decomposition rates, because of the critical role that macro-decomposers can play, for decomposition (Hassall *et al.* 1987; Wardle & Lavelle 1997; Heemsbergen *et al.* 2004; Milcu *et al.* 2008; David & Handa 2010; De Oliveira *et al.* 2010). To date, the largest decomposer size class included in across-site comparisons were soil mesofauna (e.g. springtails, mites and enchytraeids) in just one global (Wall *et al.* 2008) and one pan-tropical (Powers *et al.* 2009) study. Both studies found the presence of mesofauna to increase decomposition rates, although this effect varied strongly among sites. In addition, litter species-specific quality can modify the effect of soil macrofauna on leaf litter decomposition and litter species preference can vary among different soil fauna groups (Hättenschwiler & Gasser 2005; Milcu *et al.* 2008; Vos *et al.* 2011). Thus, it is critically important to assess whether the global effect of different decomposer groups on litter decomposition is modified by litter quality, and whether it varies among different groups of decomposers.

In this paper we addressed the hypotheses that 1) litter species-specific differences in decomposition are not conserved when litter species of various origins are exposed in distinct biomes because of long-term adaptations of decomposer food webs to local litter of specific quality, 2) the inclusion of soil meso- and macrofauna accelerates decomposition rates in all biomes, while the effect of both of these fauna groups depends on litter quality; and 3) decomposition rates correlate with different sets of litter traits in each biome and the predictive traits vary accordingly depending on the access of different decomposer groups as is expected based on the two first hypotheses. We tested these hypotheses with a fully reciprocal litter transplant experiment along a large latitudinal gradient including four forest sites in the subarctic, temperate, Mediterranean and tropical biomes. From each of these sites, we included leaf litter from four locally abundant woody species yielding a total of 16 litter species that varied widely in functional traits. Effects on decomposition driven by microbes and soil microfauna, such as protozoans and nematodes, were separated from those driven by meso- and macrofauna by varying the mesh size from 50 µm to 5 mm in our custom-made field microcosms. We found a surprisingly consistent pattern in interspecific differences in decay rates across biomes. Importantly, this pattern was largely underlain by a small and specific set of litter traits.

Materials and Methods

Study sites and plant litter species

Our study was conducted in forest ecosystems at four different sites along a large latitudinal gradient in the northern hemisphere. These sites, referred to as biomes from now on, were subarctic (Sweden), temperate (the Netherlands), Mediterranean (France) and moist tropical (French Guiana) forests (see Appendix S1, in Supporting Information). In each of the four biomes, we selected four abundant native woody plant species, each of which represented a different plant functional type (N-fixer, broadleaved evergreen, and two broadleaved deciduous species with contrasting decomposability), varying widely in their decomposition rates. By selecting the same number of species from the same plant functional types at each biome and incubating them in situ in all biomes, we created a full reciprocal transplant design.

The selected species included: *Sorbus aucuparia* L., *Alnus incana* (L.) Moench, *Vaccinium vitis-idaea* L., and *Populus tremula* L. from the subarctic biome; *Salix cinerea* L., *Alnus glutinosa* (L.) Gaertn., *Ilex aquifolium* L., and *Fagus sylvatica* L. from the temperate biome; *Fraxinus angustifolia* Vahl, *Alnus glutinosa* (L.) Gaertn., *Quercus ilex* L., and *Pistacia terebinthus* L. from the Mediterranean biome; and *Qualea rosea* Aubl., *Diplotropis purpurea* (Rich.) Amshoff, *Vochysia densiflora* Spruce ex Warm. and *Eperua falcata* Aubl. from the tropical biome. The two *Alnus glutinosa* species were clearly different ecotypes as indicated by their differences in litter N, lignin, phenols and P content. The litter was collected as senesced, freshly fallen material in autumn 2007 (with the exception of *I. aquifolium*, which was collected from cut branches after simulated senescence in the laboratory), air-dried and kept in dry, dark conditions until the start of each experiment.

Experimental design

In each biome, 5 g (dried at 40 °C) of litter of each of the 16 litter species were incubated in field microcosms (PVC cylinders, 15 cm diameter, 9 cm height) to prevent litter compaction and mimic the natural situation as closely as possible. Five grams of litter per microcosm is equivalent to 283 g litter m^{-2}, which corresponds to approximately 70% of the average annual leaf litter fall across the study sites. The microcosms were placed directly on the forest floor after removing the litter layer. This assured a continuous litter layer from the inside (treatment specific litter) to the outside (naturally occurring litter) of the microcosms. We used nylon mesh windows (2 x 100 cm^2), varying in mesh size, on the sides of the microcosms to control the accessibility of different size-classes of soil fauna. The different mesh sizes were 50 μm, 1 mm, and 5 mm, allowing the access of 1) only microorganisms and microfauna, 2) micro- and mesofauna, and 3) the complete decomposer community, including macrofauna. The mesh windows were placed close to the bottom of the microcosms to allow access of soil fauna to the microcosms at the level of the surrounding litter. For all microcosms, we used a 50 μm mesh to cover the top and the bottom – in order to reduce the possibility of physical loss of litter particles and contamination with natural leaf litter fall from the canopy. In a previous study we found that moisture content of the litter was not affected by the different mesh sizes covering the sides of microcosms (data not shown). All 16 litter species were incubated with all three different decomposer communities, leading to 48 combinations, which were replicated 5 times in a randomized block design. The experiment consisted of 240 microcosms in each of the four biomes, thus comprising a total of 960 microcosms.

Microcosms were incubated around the time of natural litter fall in each biome. The incubation time, however, varied among the biomes (Appendix S1), because we aimed for a termination of the experiment at about the same stage of litter decomposition in each biome. This aim was not fully achieved due to logistic constraints. Litter decomposition was most advanced in the tropical biome, followed by the temperate, Mediterranean and the subarctic biomes (for more information, see Appendix S1). After harvest, the litter was cleaned by hand from any attached soil particles before dry weight (65 °C) was determined. To enable comparisons among the biomes, data were standardized by calculating the annual decomposition rate constant (k yr^{-1}):

$$k = -\frac{\ln\left(\frac{M_t}{M_0}\right)}{t}$$

where M_t = final mass, M_0 = initial mass converted to equivalent mass at 65 °C, and t = incubation time (in years). Using k, we assumed a first order exponential decay for all litter species. It should be noted that the use of k may have affected our results as the decomposition phases varied among litter species and biomes. Considering a normal biphasic nature of decomposition process, our results may overestimate the decomposition rates of the slowly decomposing species and especially in biomes where decomposition had not proceeded far, and vice versa underestimate the rates of the fast decomposing species and especially in biomes where decomposition had proceeded further. An alternative option to standardize litter decomposition rates at the different biomes is to use relative mass loss (observed mass loss divided by the mean mass loss of all litter species in a given biome). However, this option does not allow a comparison between the effects of all three factors: litter identity, decomposer communities and biome, on litter decomposition.

Plant litter traits

Differences in litter quality were characterized by 26 widely-used, but rarely assessed within the same study, chemical and physical traits. Chemical traits included pH, concentrations (expressed as % dry matter or d.m.) of carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), the carbon fractions of cellulose, hemicellulose, lignin, total phenols, soluble phenols, condensed tannins, and total water soluble compounds; and the ratios of C/N, C/P, lignin/N, lignin/P, phenols/N and phenols/P. The physical traits included leaf toughness (g H_2O), leaf tensile strength (N cm^{-1}), specific leaf area (SLA: cm^2 g^{-1}), leaf water saturation (% H_2O d.m.) and three-dimensionality (total leaf surface area per volume: cm^2 cm^{-3}). Details about trait measurements are in Appendix S2. The distribution of variation among all plant litter traits across all litter species was visualized by a Principle Component Analysis (PCA: Fig. 1). PCA ordination characterizes and partly separates the litter species according to their biome of origin. Litter traits (26 levels) were used as the response variables and litter species (16 levels: mean decomposition rate constant per litter species) as 'samples'. PCA was conducted by Canoco for Windows version 4.5 (ter Braak & Šmilauer 2002).

Data analysis

Decomposition rate constants were $\log_{10}$-transformed to ensure homogeneity of variance. Prior to the main analyses, we tested the effect of block for each biome separately in a one-way ANOVA. Since the effect of block was not significant for any biome, we excluded the

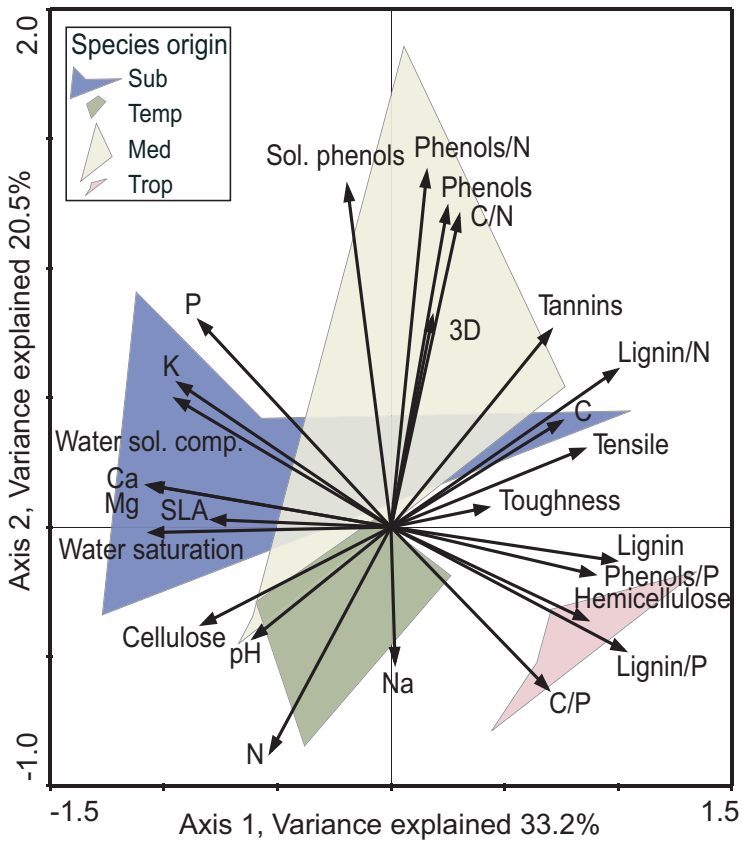

Figure 1. Principal Component Analysis (PCA) ordination of 26 litter traits (arrows) and the 12 litter species (minimal polygon/ distorted rectangular) arranged by their origins (four species per biome: Subarctic, Temperate, Mediterranean or Tropical). The traits were centered and standardized prior to ordination.

term block from further analyses.

Our fully balanced design assessing the effects of all combinations of litter species identity, decomposer community and biome and their interactions on litter decomposition rates was analysed in a full factorial ANOVA with each variable as a fixed factor (total df=950). Given the greater probability of detecting statistical significance for small effects when large datasets are analysed, the effect size of the main effects and the interactions in explaining the variance in decomposition rate constants was calculated as the classical eta squared (η^2) and omega squared (ω^2) from the ANOVA results. As the results for all main effects and their interactions differed less than 0.5% between the η^2 and ω^2, and the ω^2 cannot be calculated for residuals, we only report η^2. Statistically significant ($P < 0.05$) main effects and interactions were analyzed further using HSD *post hoc* tests. As data transformations can make non-additive effects seem additive, we ran the ANOVA also with the untransformed data for comparison (Appendix S3), despite the fact that the ANOVA model with untransformed data did not fill the data requirements.

Additionally, we specifically tested whether the interactions between biome and litter identity were caused by decomposers favouring locally-grown litter species over foreign litter. The observed mass loss per species as well as the decomposition rate constant was used. Both k and mass loss were expressed relative to the mean value of all litter species incubated in

a given biome according to Ayres *et al.* (2009). Due to this standardization, the main effect of biome has become redundant. A full factorial ANOVA tested the effects of biome, litter origin and different decomposer communities and all their interactions. Log_{10}-transformation ensured the homogeneity of variance in both dependent variables and did not affect the significance of the interactions. For this analysis, we were particularly interested in the interaction between biome and litter origin on litter decomposition.

The degree to which the combinations of litter traits could account for observed decomposition rate constants was tested separately for each combination of biome and decomposer community. This separation into 12 datasets was done to assess the consistency in contributing litter traits across the datasets. The relationship between the 26 litter traits and the interspecific decomposition rate constant was assessed by two methods, AIC_c (Hurvich & Tsai 1989; Burnham & Anderson 2002) and forward stepwise multiple linear regressions. Model selection was very similar among the two methods and therefore, only the regression coefficients are presented. Prior to the analysis, traits for which the linear relation to decomposition rate constants could be improved were log_{10}-transformed. After model selection, we checked each of these models for collinearity among the significant traits as determined by the Variation Inflation Factor (set to a limit of VIF<4). When collinearity was observed, the collinear trait which lowered most the fit of the model was omitted from the subsequent model. These subsequent models are presented as the optimal trait model with free trait selection. As a final step, we determined the relationship between the decomposition rate constants and the fixed set of traits that had given the highest fit across all datasets in the optimal trait models. In comparison to the individual optimal trait models, this final step assessed the control of the same traits on litter decomposition in all datasets. Regression results are reported as adjusted r^2 to allow comparison between models with a different number of explanatory variables. All analyses were performed with SPSS version 20.0.0 (SPSS Inc., Chicago, IL, USA).

Results

Consistent interspecific ranking of decomposability across biomes

We found strong differences in mean decomposition rate constants (k) among biomes, litter species and decomposer communities (Fig. 2). The mean k-values ranged from 0.03 to 5.66 yr^{-1}.

Table 1. Results of a full factorial ANOVA analysis on decomposition rate constant k per year (total df=950). Degrees of freedom (df), Type III sum of squares (SS), mean square (MS), F statistic (F), statistical significance (*P*), and variance explained (Var. expl. (%)) are given for all the main effects: biome, litter species identity (identity) and decomposer community, which was assessed by a varying mesh size (mesh); and their two-way and three-way interactions.

Effect	df	SS	MS	F	*P*	Var. expl. (%)
Biome	3	137.3	45.76	4821.4	<0.001	59.4
Identity	15	78.9	5.26	553.9	<0.001	34.1
Mesh	2	0.1	0.05	5.8	0.003	0.0
Biome * Identity	45	2.2	0.05	5.2	<0.001	1.0
Biome * Mesh	6	2.5	0.42	43.7	<0.001	1.1
Identity * Mesh	30	1.3	0.04	4.7	<0.001	0.6
Biome * Identity * Mesh	90	1.6	0.02	1.8	<0.001	0.7
Residuals	759	7.2	0.01			3.1

As expected, biome explained most of the variance (59%). Mean k-values were highest in the tropical biome (2.11 ± 0.11), and they were 68%, 78% and 92% lower in temperate, Mediterranean and subarctic biomes, respectively. However, litter species identity also had a strong effect (34% variance explained: Table 1). As a consequence, the main effect of litter species identity was much stronger than any of its interactions with biome and/or decomposer community. Despite the large differences in k-values among biomes, the relative differences in k-values among all 16 litter species were largely conserved across biomes, resulting a surprisingly consistent pattern. Several litter species that originated from subarctic, temperate or Mediterranean forests, such as *Sorbus*, *Ilex*, *Fraxinus* or *Alnus*, were among the most rapidly decomposing species in all biomes, whereas the most slowly decomposing litter species in all biomes *Vochysia*, *Eperua* and *Diplotropis* originated from the tropical forest (Fig. 2, Fig. S4.1 in Appendix). Similarly, the PCA analysis showed an overlap of subarctic, temperate and Mediterranean species in trait space, while the tropical species were separated, based on a particularly low concentration in P, K and water soluble compounds, and a high lignin and hemicellulose content (Fig 1).

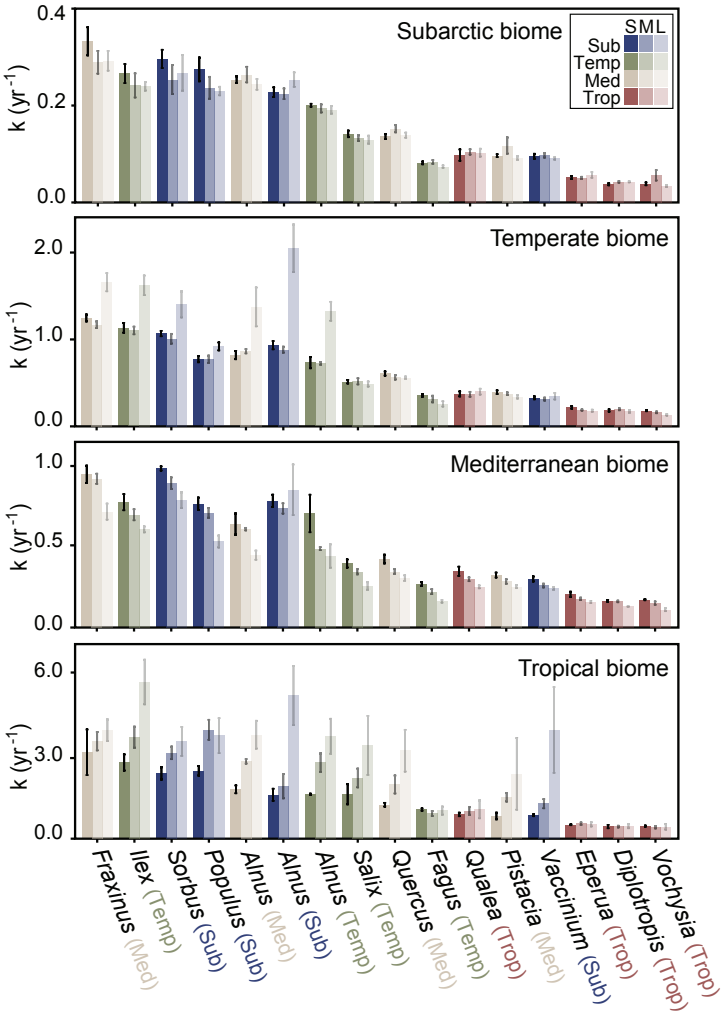

Figure 2. Average decomposition rate constants (k) per year (yr^{-1}) ± standard error of the mean (SEM) for each plant litter species incubated in subarctic, temperate, Mediterranean and tropical biomes. Bar colour and the abbreviation after the species name indicates the origin of plant litter species. Bar shade indicates the decomposer community that was assessed by varying mesh size (Small, Medium or Large mesh). Litter species are shown in descending order based on the average k in small mesh size treatments in all biomes. Note, that the scale for k is different in each biome.

Furthermore, the ranking of all 16 litter species, based on mass loss, remained basically the same in all biomes regardless of the biome of origin of litter species. Accordingly, we found that the relative decomposition of a litter of a given origin did not vary among biomes and thus there was no evidence that litter decomposes faster in its home biome than in the foreign biomes (when the data was assessed either as relative k or mass loss) (Table 2, Fig 3). Instead we found that the decomposition of tropical species was lower compared to the decomposition of litter of any other origin in all biomes (the significant main effect of litter origin, Table 2).

The varying role of decomposer community complexity across biomes

Unlike litter species identity, the main effect of decomposer community was weak and showed a stronger interaction with biome (Table 1). When analysed for each biome separately, the effect of decomposer community complexity was only significant in the tropics (Fig. 2, Fig. S4.2 in Appendix) and only between the complete (large mesh size) and the most reduced (smallest mesh size) decomposer communities. In the tropical biome, the k-values were on average 95.1% higher in the large mesh size microcosms compared to microcosms with the smallest mesh size. There was a trend for a similar mesh size effect in the temperate biome, although it was restricted to fewer litter species than in the tropics. The three-way interaction of decomposer community

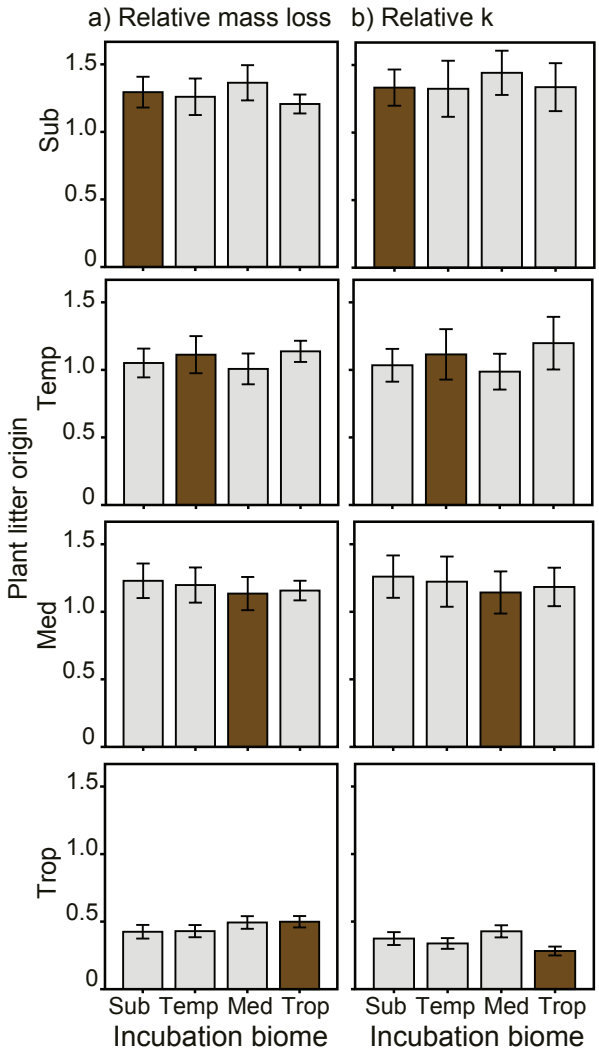

Figure 3. Average relative (to the mean value of all litter species in a given biome) a) decomposition rate constants k and b) mass loss ± standard error of the mean (SEM) of subarctic, temperate, Mediterranean and tropical litter species (plant litter origin) incubated in subarctic, temperate, Mediterranean and tropical biomes. Dark bars show litter incubated in its biome of origin and light bars show litter incubated in foreign biomes. Litter species were always incubated with three different decomposer communities, thus n = 12 (4 litter species per origin x 3 decomposer communities).

Table 2. Results of two full factorial ANOVA analyses of average relative (to the mean value of all litter species incubated in a given biome) a) decomposition rate constant (k) and b) mass loss, per litter species (total df = 191 in both analyses). Degrees of freedom (df), Type III sum of squares (SS), mean square (MS), F statistic (F) and statistical significance (*P*) are given for all the main effects: biome, litter origin and decomposer community, which was assessed by a varying mesh size (mesh); and their two- and three-way interactions.

Effect	df	SS	MS	F	*P*
a) Relative k					
Native vs. foreign	1	0.0	0.0	0.6	ns
Biome	3	1.3	0.4	5.8	0.001
Mesh	2	0.0	0.0	0.1	ns
Native vs. foreign * Biome	3	4.1	1.4	17.9	<0.001
Native vs. foreign * Mesh	2	0.0	0.0	0.2	ns
Biome * Mesh	6	0.3	0.1	0.7	ns
Native vs. foreign * Biome * Mesh	6	0.1	0.0	0.2	ns
Residuals	168	12.9	0.1		
b) Relative mass loss					
Native vs. foreign	1	0.0	0.0	0.1	ns
Biome	3	0.3	0.1	2.0	ns
Mesh	2	0.0	0.0	0.0	ns
Native vs. foreign * Biome	3	1.8	0.6	12.1	<0.001
Native vs. foreign * Mesh	2	0.0	0.0	0.0	ns
Biome * Mesh	6	0.1	0.0	0.3	ns
Native vs. foreign * Biome * Mesh	6	0.0	0.0	0.1	ns
Residuals	168	8.4	0.1		

with litter identity and biome was relatively strong compared to the main effect of decomposer community. It showed that litter in microcosms with larger mesh sizes had higher k-values in tropical and temperate biomes, whereas it had lower k-values in the Mediterranean biome (Fig 2). In the subarctic biome, only two (*Vochysia* and *Pistacia*) out of 16 litter species showed mesh size effect. Importantly, litter species for which k-values were most strongly affected by the decomposer community in a given biome, were not necessarily the litter species originating from that biome (Fig. 2). This observation was particularly striking for tropical litter species decomposing at their site of origin. Access to the full decomposer community did not stimulate decomposition in any of the four native litter species, while all foreign litter species except one (*Fagus*), showed substantial fauna-driven increases in decomposition rates.

Traits underlying the interspecific pattern in decomposition rates

The trait regressions supported and explained the overall consistency in the interspecific pattern of k-values across biomes (Table 3). Altogether 13 out of the 26 traits contributed significantly to the interspecific variation in k-values in at least one of the datasets. Eight out of 12 datasets (all small mesh sizes, subarctic, temperate and Mediterranean medium mesh size, and subarctic large mesh size), had the same two or three of the following traits showing the strongest relation to the k-values: Mg concentration, litter water saturation and concentration of tannins (Table 3). In contrast, four datasets deviated from the consistent eight datasets. The tropical medium mesh size and Mediterranean large mesh size only had Mg concentration or Mg and Ca concentration as significant explanatory variables, respectively. In contrast, the two remaining datasets (tropical and temperate large mesh size) had very different sets of significant explanatory variables (see Table 3). Consequently, when k-values were regressed with a fixed trait selection consisting

Table 3. Results of linear regressions (given as adjusted r^2 (Adj. r^2)) of the k-value of each litter species, with the litter traits as independent variables in a) free or b) fixed trait selection models. The free selection models were run by forward stepwise method and the fixed trait selection models where the most parsimonious set of traits was fitted to each dataset were run by simultaneous method. *N* = 16 for each dataset in all models. Trait names are given in full or by their chemical symbol except: Wat sat = water saturation capacity, 3D = three-dimensionality, Wat sol compounds = water soluble compounds.

		a) Free trait selection		b) Fixed trait selection	
Biome	**Mesh**	**Adj. r^2**	**Independent variables**	**Adj. r^2**	**Independent variables**
SUB	S	0.94	Mg, Wat sat, Tannins, 3D	0.89	Mg, Wat sat, Tannins
	M	0.91	Mg, Tannins, Wat sat, Soluble phenols	0.84	Mg, Wat sat, Tannins
	L	0.88	Wat sat, Tannins, Soluble phenols	0.88	Mg, Wat sat, Tannins
TEMP	S	0.95	Mg, Tannins, Wat sat, Tensile, Hemicellulose	0.84	Mg, Wat sat, Tannins
	M	0.96	Mg, Tannins, Wat sat, Tensile, Hemicellulose	0.86	Mg, Wat sat, Tannins
	L	0.92	Lignin/N, 3D, pH, Wat sol compounds	0.79	Mg, Wat sat, Tannins
MED	S	0.96	Wat sat, Mg, Tannins, 3D	0.89	Mg, Wat sat, Tannins
	M	0.98	Wat sat, Mg, Tannins, 3D, Phenols/P, Wat sol compounds	0.89	Mg, Wat sat, Tannins
	L	0.77	Mg, Ca	0.78	Mg, Wat sat, Tannins
TROP	S	0.75	Mg, Wat sat	0.81	Mg, Wat sat, Tannins
	M	0.68	Mg	0.75	Mg, Wat sat, Tannins
	L	0.81	Phenols/P, Hemicellulose, Toughness	0.52	Mg, Wat sat, Tannins

of Mg concentration, water saturation and concentration of tannins (as these were the three traits showing the highest regression to k-values across all 12 datasets), the greatest reduction in explained variance compared to the free trait selection models occurred in the tropical and temperate large mesh size datasets. The relationships between k-values and traits are visualized in Appendix S5.

Discussion

Our fully reciprocal litter transplant study is unique as it is the first experiment conducted with a large number (16) of leaf litter species and three different decomposer community complexities across four biomes with a balanced representation of biome-specific litter species. We found surprisingly consistent patterns in interspecific differences in litter decomposition rates across biomes. Furthermore, this consistent pattern could to a large extent be attributed to a small set of common litter functional traits.

A consistent effect of litter species identity

In contrast to our first hypothesis, the effect of litter identity was strong and consistent across biomes. Litter identity explained 34% of total variation, whereas all interactions with other factors (including biome) together explained only 2% of the variation. Remarkably, tropical litter species generally decomposed slower than all other litter species, even at their site of origin. This finding supports the argument that leaf litter from tropical trees share a litter trait-syndrome of poor carbon quality that strongly limits decomposer activity (Hättenschwiler *et al.* 2011).

The global-scale consistent interspecific pattern in decomposition rates reported here is in line with a previous smaller scale transplant study of Cornelissen *et al.* (1999). However, in that study, litter of 16 species from Argentina was incubated in artificial, standardized litter beds at two sites (Argentina and the UK). Here we assessed decomposition under widely varying climatic conditions in undisturbed forest ecosystems following a reciprocal design. The interspecific consistency we observed suggests that decomposer organisms across a large latitudinal gradient

(subarctic to tropical forest) with widely different general environmental constraints, respond almost identically to litter quality variation and appear not to be specialized on native litter material.

Indeed, we observed no difference in relative decomposition among biomes for any litter origin. This finding provides clear evidence that "home grown food" was not preferred by the decomposer communities. It contradicts the hypothesized mechanism (adaptation) underlying the interaction between site and litter identity in two previous large-scale transplant studies (Gholz *et al.* 2000; Zhou *et al.* 2008). These contrasting results may be due to the fact that in contrast to our study, Gholz *et al.* (2000) used only two litter species and Zhou *et al.* (2008) only one common substrate, the decomposition of which was compared to the local litter types. Our study with 16 litter species in four biomes found that the effect of litter identity is not strongly affected by biome differences in environmental factors and decomposer communities. Instead, decomposition was determined by general litter quality aspects. These findings suggest that decomposers actually show little adaptation to a recurrent input of a particular litter quality, but instead can respond quickly to changes in litter quality.

A weak effect of the decomposer community composition

By using three different mesh sizes in four biomes, we are the first to show that at a global scale, the effect of decomposer community complexity on the decomposition rates was generally weak, but depended on biome and litter identity. This result provided only partial support for our second hypothesis, stating that the access of soil meso- and macrofauna accelerates decomposition. The effect of decomposer community complexity was significant only in the tropical biome, but there decomposition rate constants were almost twice as high with the most complete decomposer community compared to the community consisting of only microorganisms and microfauna (i.e. smallest mesh size). A similar trend was visible in the temperate biome, but for fewer litter species than in the tropical biome. Unlike hypothesized, decomposer communities including meso- and macrofauna did not always accelerate decomposition of litter species (especially in the subarctic and Mediterranean biome), and in the Mediterranean and temperate biome, they even slowed down the decomposition of some litter species. These results support earlier findings by Wall *et al.* (2008), who showed that larger decomposers play an important role for decomposition only under the most favourable climatic conditions. Nevertheless, our results have to be interpreted with caution because the stage of decomposition was different among biomes. Perhaps the effect of meso- and macrofauna becomes evident only in the later stages of decomposition, when the litter has been processed further and is strongly colonized by microorganisms. Preference for partially decomposed over freshly fallen leaf litter has been documented for woodlice (Zimmer 2002), earthworms (Edwards & Bohlen 1995) and millipedes (De Oliveira *et al.* 2010) (but see Smith and Bradford 2003). Thus, effects of larger fauna on decomposition may have been missed in the higher latitude sites of our study due to the relatively early stage of decomposition at the time of harvest. However, the strength of any potential fauna effect would depend on the abundances and body size of the local soil fauna that are known to decrease from the equator to the poles (Swift *et al.* 1979).

Consistent litter trait control over decomposition

Plant litter quality and soil nutrient limitation of decomposers are documented to vary strongly among different biomes (Swift *et al.* 1979; Aerts 1997; Freschet *et al.* 2011). Consequently, we expected litter traits that correlate best with decomposition to vary among the four different biomes. However, we observed a surprisingly similar common set of litter traits correlating with decomposition across biomes and most of the decomposer complexity treatments, particularly when macrofauna had been excluded. We identified a set of three litter traits (Mg concentration, water saturation capacity and the concentration of condensed tannins), which could explain most of the variation in decomposition rates. In contrast to the two previous large spatial scale litter transplant studies (Trofymow *et al.* 2002; Currie *et al.* 2009), lignin/N ratio explained relatively little variation in decomposition rates in our study. It might at first sight be surprising that neither lignin/N ratio nor other common leaf economic spectrum traits were among the traits giving the highest explanatory power. However, the control of concentrations of Mg and other cations (Nicolai 1988; Cornelissen & Thompson 1997; Kaspari *et al.* 2009) and tannins (Kraus *et al.* 2003; Coulis *et al.* 2009; Coq *et al.* 2010) on decomposition has been shown previously. Mg is an essential element in the fauna diet as it is needed in enzymatic reactions, nerve connections, muscle function and skeleton formation (National Research council 2005). Tannins are known to slow down decomposition as they can be unpalatable to decomposers through their toxicity or by binding with dietary proteins or digestive enzymes (Coulis *et al.* 2009, Coq *et al.* 2010). Similarly, litter physical traits also influence decomposition (Swift *et al.* 1979; Cornelissen 1996; Cornelissen *et al.* 1999; Pérez-Harguindeguy *et al.* 2000; Vaieretti *et al.* 2005; Santiago 2007), but except for specific leaf area (SLA), they typically have not been considered in global litter transplant studies. In our study, litter water saturation was the second strongest predictor of decomposition, but it showed high collinearity with SLA. We suggest that litter water saturation strongly controls the microclimate for decomposers as it determines water acquisition and retention.

Although these three traits, either directly or indirectly, best explained the interspecific decomposition rates in the majority of decomposer treatments in all four biomes, we did observe clear deviations from the dominant trait control over decomposition rates in support of our third hypothesis. These deviations were particularly apparent with the most complete decomposer community in the tropical and temperate biome. In these two cases, the set of traits that best explained variation in decomposition rates across litter species showed no overlap with the common set identified for most datasets nor with each other. Thus, trait control in the presence of the most complete decomposer communities in the tropical and temperate biome did not only deviate from microbially dominated decomposition, but it also differed between these biomes. Our results point to different constraints of macro-decomposers in tropical and temperate biomes, which may reflect the fact that the identity of the dominant macro-decomposer species differs between the temperate and tropical biome (Swift *et al.* 1979; Giller 1996).

In conclusion, our results show strong evidence for constant relative differences in decomposition among vastly different litter types across distinct biomes regardless of the leaf litter origin. These differences were closely linked to a small set of three litter traits, suggesting that decomposer communities respond largely identically to resource quality heterogeneity in very different

biomes with little specialization to site-specific litter types. Collectively, our data provide strong support for using trait-based approaches in modelling the decomposition component of global-scale biosphere-atmosphere carbon fluxes. The fact that a low number of litter traits is sufficient to explain variation in decomposition, suggests the possibility of developing a relatively simple model to incorporate decomposition and organic matter quality in plant-atmosphere feedbacks.

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References

Aerts R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos, 79, 439-449.

Ayres E., Steltzer H., Simmons B., Simpson R., Steinweg M., Wallenstein M., *et al.* (2009). Home-field advantage accelerates leaf litter decomposition in forests. Soil Biol. Biochem., 41, 606-610.

Berg B., Berg M.P., Bottner P., Box E., Breymeyer A., Anta R.C.d., *et al.* (1993). Litter mass loss in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. Biogeochemistry, 20, 127-153.

Brovkin, V., P.M. van Bodegom, Kleinen T., Wirth C., Cornwell W.K., Cornelissen J.H.C. *et al.* (2012). Plant-driven variation in decomposition rates improves projections of global litter stock distribution. Biogeosciences 9: 565–576

Burnham K.P. & Anderson D.R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2 edn. Springer-Verlag, New York.

Cadish G. & Giller K.E. (eds.) (1997). Driven by nature, plant litter quality and decomposition. CAB international, Wallingford.

Chapin III F.S, McFarland J., McGuire A.D., Euskirchen E.S., Ruess R.W. & Kielland K. (2009). The changing global carbon cycle: linking plant-soil carbon dynamics to global consequences. J. Ecol., 97, 840-850.

Coq S., Souquet J.-M., Meudec E., Cheynier V. & Hättenschwiler S. (2010). Interspecific variation in leaf litter tannins drives decomposition in a tropical rain forest of French Guiana. Ecology, 91, 2080-2091.

Cornelissen J.H.C. (1996). An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J. Ecol., 84, 573-582.

Cornelissen J.H.C., Perez-Harguindeguy N., Diaz S., Grime J.P., Marzano B., Cabido M., *et al.* (1999). Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. New Phytol., 143, 191-200.

Cornelissen J.H.C. & Thompson K. (1997). Functional leaf attributes predict litter decomposition rate in herbaceous plants. New Phytol., 135, 109-114.

Cornwell W.K., Cornelissen J.H.C., Amatangelo K., Dorrepaal E., Eviner V.T., Godoy O., *et al.* (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett., 11, 1065-1071.

Coulis M., Hättenschwiler S., Rapior S. & Coq S. (2009). The fate of condensed tannins during litter consumption by soil animals. Soil Biol. Biochem., 41, 2573-2578.

Currie W.S., Harmon M.E., Burke I.C., Hart S.C., Parton W.J. & Silver W. (2009). Cross-biome transplants of plant litter show decomposition models extend to a broader climatic range but lose predictability at the decadal time scale. Global Change Biol., 16, 1744-1761.

David J.-F. & Handa I.T. (2010). The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. Biol. Rev., 85, 881-895.

De Oliveira T., Hättenschwiler S. & Handa I.T. (2010). Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. Funct. Ecol., 24, 937-946.

Edwards C.A. & Bohlen P.J. (1995). Biology and Ecology of Earthworms. Chapman and Hall, London.

Freschet G.T., Dias A.T.C., Ackerly D.D., Aerts R., van Bodegom P.M., Cornwell W.K., *et al.* (2011). Global to community scale differences in the prevalence of convergent over divergent leaf trait distributions in plant assemblages. Global Ecol. Biogeogr. 20, 755-765.

Gholz H.L., Wedin D.A., Smitherman S.M., Harmon M.E. & Parton W.J. (2000). Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biol., 6, 751-765.

Giller P.S. (1996). The diversity of soil communities, the 'poor man's tropical rainforest'. Biodivers. Conserv., 5, 135-168.

Hassall M., Turner J.G. & Rands M.R.W. (1987). Effects of terrestrial isopods on the decomposition of woodland leaf litter. Oecologia, 72, 597-604.

Hättenschwiler S., Coq S., Barantal S. & Handa I.T. (2011). Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis. New Phytol., 189, 950-965.

Hättenschwiler S. & Gasser P. (2005). Soil animals alter plant litter diversity effects on decomposition. PNAS, 102, 1519-1524.

Heemsbergen D.A., Berg M.P., Loreau M., van Hal J.R., Faber J.H. & Verhoef H.A. (2004). Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science, 306, 1019-1020.

Hunt H.W., Ingham E.R., Coleman D.C., Elliott E.T. & Reid C.P.P. (1988). Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. Ecology, 69, 1009-1016.

Hurvich C.M. & Tsai C.-L. (1989). Regression and time series model selection in small samples. Biometrika, 76, 297-307.

Kaspari M., Yanoviak S.P., Dudley R., Yuan M. & Clay N.A. (2009). Sodium shortage as a constraint on the carbon cycle in an inland tropical rainforest. PNAS, 106, 19405-19409.

Kraus T.E.C., Dahlgren R.A. & Zasoski R.J. (2003). Tannins in nutrient dynamics of forest ecosystems - a review. Plant Soil, 256, 41-66.

Milcu A., Partsch S., Scherber C., Weisser W.W. & Scheu S. (2008). Earthworms and legumes control litter decomposition in a plant diversity gardient. Ecology, 89, 1872-1882.

National Research Council (2005). Mineral Tolerance of Animals (2nd rev. ed.). National Academic Press, Washington.

Nicolai V. (1988). Phenolic and mineral content of leaves influences decomposition in European forest ecosystems. Oecologia, 75, 575-579.

Pérez-Harguindeguy N., Díaz S., Cornelissen J., Vendramini F., Cabido M. & Castellanos A. (2000). Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. Plant Soil, 218, 21-30.

Powers J.S., Montgomery R.A., Adair E.C., Brearley F.Q., DeWalt S., J. , Castanho C.T., *et al.* (2009). Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. J. Ecol., 97, 801-811.

Santiago L.S. (2007). Extending the leaf economics spectrum to decomposition: evidence from a tropical forest. Ecology, 88, 1126-1131.

Smith V.C. & Bradford M.A. (2003). Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. Appl. Soil Ecol., 24, 197-203.

Swift M.J., Heal O.W. & Anderson J.M. (1979). Decomposition in terrestrial ecosystems. Blackwell Scientific Publications, Oxford.

ter Braak C.J.F. & Šmilauer P. (2002). CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (ver. 4.5). In. Microcomputer Power New York.

Trofymow J.A., Moore T.R., Titus B., Prescott C., Morrison I., Siltanen M., *et al.* (2002). Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can. J. For. Res., 32, 789-804.

Vaieretti M., Pérez Harguindeguy N., Gurvich D., Cingolani A. & Cabido M. (2005). Decomposition dynamics and physico-chemical leaf quality of abundant species in a montane woodland in central Argentina. Plant Soil, 278, 223-234.

Vos V.C.A., van Ruijven J., Berg M.P., Peeters E.T.H.M. & Berendse F. (2011). Macro-detritivore identity drives leaf litter diversity effects. Oikos, 120, 1092-1098.

Wall D.H., Bradford M.A., St. John M.G., Trofymow J.A., Behan-Pelletier V., Bignell D.E., *et al.* (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Global Change Biol., 14, 2661-2677.

Wardle D.A. & Lavelle P. (1997). Linkages between soil biota, plant litter quality and decomposition. In: Driven by nature: plant litter quality and decomposition (eds. Cadish G & Giller KE). CAB International, Wallingford, pp. 107-124.

Zhang D., Hui D., Luo Y. & Zhou G. (2008). Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J. Plant Ecol., 1, 85-93.

Zhou G., Guan L., Wei X., Tang X., Liu S., Liu J., *et al.* (2008). Factors influencing leaf litter decomposition: an intersite decomposition experiment across China. Plant Soil, 311, 61-72.

Zimmer M. (2002). Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach. Biol. Rev., 77, 455-493.

Supporting information: Appendices S1-S5

Appendix S1: Details on experimental sites and litter incubation

Table S1. Running time of the experiments in each biome and the general climatic conditions during the experiments. Running time of the experiments (days #), mass loss (%) that the fastest decomposing litter species reached at the end of the experiment (max) and average mass loss at the end of the experiment (mean) is given for each site (biome). Precipitation is given in two units, of which the first (mm) expresses the precipitation during the incubation time, and the second (mm/year) is the previous precipitation expressed per year.

					Mass loss (%)						
					Max	Mean	Air temperature (°C)			Precipitation	
Biome	Coordinates	Start date	End date	Days #	Mean±SE	Mean±SE	Mean	Max	Min	(mm)	(mm/year)
SUB Sweden	68° 21'N, 18° 40'E	12/09/08	03/09/10	722	43.7±2.4	25.9±0.8	-0.3	26.6	-31.5	505	255
TEMP the Netherlands	52° 18'N, 5° 41'E	25/06/08	27/03/09	276	77.2±3.5	36.7±1.2	8.4	32.5	-15.4	569	752
MED France	43° 23'N, 2° 51'E	24/10/08	12/08/09	293	48.1±5.7	28.9±0.9	13.5	37.7	-5.1	648	807
TROP French Guiana	5° 18'N, 52° 55'W	27/08/07	30/04/08	248	96.1±2.2	63.8±1.6	25.1	33.3	17.5	1974	2905

Appendix S2: Trait analysis methods

Table S2. Methods used in the trait analyses. All chemical traits were analyzed from 3 subsamples per litter species from grinded heterogeneous material. The physical traits (water saturation, toughness, SLA and tensile strength) were measured from 10 leaves per species, except three-dimensionality was measured with numerous leaves and its' measurement was replicated 10 times.

Trait	Method
N, C	Analysed with Thermo-Finningan NC EA 1112 elementary analyser (Strada Rivoltana, Milan, Italy)
Lignin, cellulose, hemicellulose, water soluble compounds	Material was analysed by a fiber analyzer (Fibersac 24, Ankom, Macedon, New Jersey, USA) in a classical fiber analysis, the method is further described in: van Soest, P.J. (1963). Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. *Journal of the Association of Official Analytical Chemists*, 46: 829–835.
Total phenols, soluble phenols	Total phenolics were measured colorimetrically with the Folin-Ciocalteau reagent by using gallic acid as a standard. For soluble phenolics, 1 g of sample was extracted with 60 mL of water, and for total phenolics, 1 g of sample was extracted with 60 mL of 50% methanol and then shaken for 2 h and filtered (filter number 112, Durieux, Torcy, France). The method is further described in: Marigo, G. (1973). Sur une me´thode de fractionnement et d'estimation des compose´es phe´noliques chez les ve´ge´taux. *Analusis* 2:10–110.
Condensed tannins	Butanol-HCl method according to: Porter L.J, Hirstich L.N., Chan B.G.(1986) The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin. *Phytochemistry*, 25: 223–230. and Waterman, P.G. & Mole, S. (1994). Analysis of Phenolic Plant Metabolites. Blackwell Scientific Publications, Methods in Ecology. Oxford.
P, K, Ca, Mg and Na	Litter samples were digested with sulphuric acid, salicylic acid, hydrogen peroxide and selenium. Phosphorus concentrations were measured colorimetrically, using a segmented flow analyzer (SKALAR SAN Plus System, the Netherlands). Potassium, calcium, magnesium and sodium were measured by flame atomic emission spectroscopy (Varion SpectrAA-600, the Netherlands). The digestion is further described in: Novozamsky, I., Houba, V. J. G., van Eck, R. & van Vark, W. (1983) Comm. Soil Sci.Plant Anal. 14: 239-249
pH	Analysis described in: Cornelissen et al. (2006) Foliar pH as a new plant trait: can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types? *Oecologia*, 147: 315-326
Toughness	1.5 mm needle was used. Analysis is described in : Graça, M.A.S. & Zimmer, M. (2004) Leaf toughness. Methods to Study Litter Decomposition: A Practical Guide (eds M.A.S. Graça, F. Bärlocher & M.O. Gessner), pp.109–113. Kluwer Academic Publishers, Netherlands.
Water saturation	Water saturation was analysed by placing the leaves in a large plastic container (volume ~ 400 cm^3) with a non-hermetic lid. The leaves were sprayed three times per day with a 1 ml of fine mist of water. Leaves were weighed after 48 hours. The wet weight was compared to the dry weight.
SLA	Leaves were measured with an area meter (MK2; Delta-T, Cambridge, England) and subsequently dried at 65ºC for 48 hours to obtain the dry mass.
Three-dimensionality	Analysed by counting the number of leaves fitted into a known volume without packing or arranging leaves. The volume of the container was adapted to the average size of the leaf. Expressed as leaf surface area per volume by converting the leaf number to leaf total surface area (2 x average projected leaf area), which was determined by the SLA measurements.
Tensile strength	Air dry leaves were remoistened for 18 hours. After this the excess water was wiped away from the leaf surface by an absorbent tissue. First the mid-vein was removed and after that a longitudinal stripe was cut from one side of the leaf. This stripe was cut from the area adjacent to the mid-vein, and varied in width according to the leaf size. The width was 3, 5, 10 or 20 mm depending on the species. Measurements were done always in longitudinal direction from the broadest part of the leaf. Measurements were made by Mecmesin Ultratest with an AFG 1000 N, Advanced Force Gauge (Mecmesin, Broadbridge , UK) with Thümler TH227 clamps. Distance between the clamps was always 2 mm.

Appendix S3: ANOVA model with untransformed data

Table S3. Results of a full factorial ANOVA analysis on decomposition rate constant k, which was untransformed (total df=950). Degrees of freedom (df), Type III sum of squares (SS), mean square (MS), F statistic (F), statistical significance (P), and variance explained (Var. expl. (%)) are given for all the main effects: biome, litter species identity (identity) and decomposer community, which was assessed by a varying mesh size (mesh); and their two-way and three-way interactions. These results should be interpreted cautiously as the data assumptions were not met as is seen in the figure S3 below.

Effect	df	SS	MS	F	*P*	Var. Expl. (%)
Biome	3	531.1	177.0	578.9	<0.001	41.3
Identity	15	201.0	13.4	43.8	<0.001	15.6
Mesh	2	22.5	11.2	36.7	<0.001	1.7
Biome * Identity	45	160.2	3.6	11.6	<0.001	1.2
Biome * Mesh	6	58.9	9.8	32.1	<0.001	4.6
Identity * Mesh	30	24.2	0.8	2.6	<0.001	1.8
Biome * Identity * Mesh	90	48.1	0.5	1.7	<0.001	3.7
Residuals	759	232.1	0.3			18.0

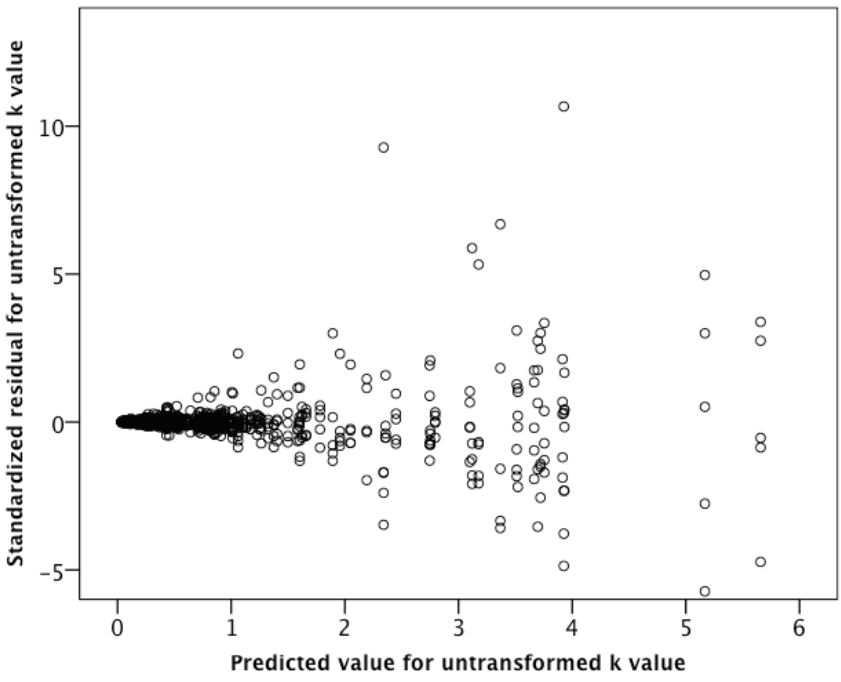

Figure S3. Predicted value versus standardized residuals of the ANOVA analysis shown above in Table S3.

Appendix S4: Identity and biome x mesh size effect on k

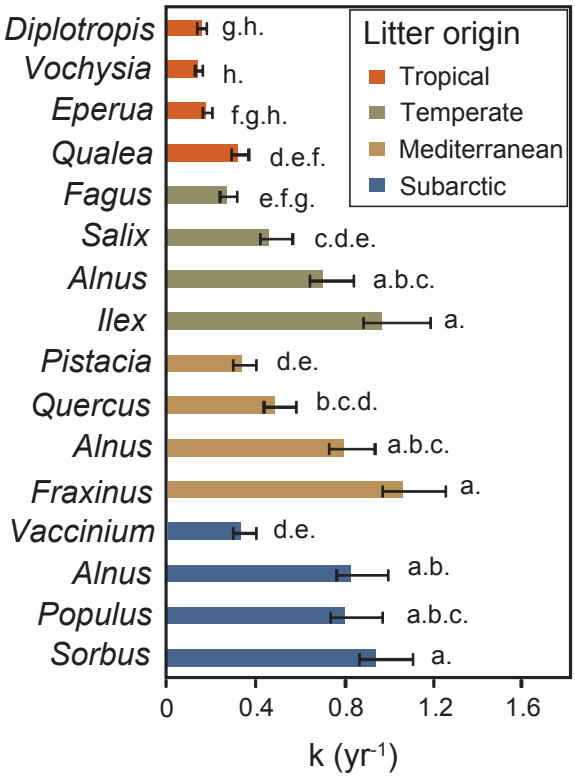

Figure S4.1. Average back-transformed decomposition rate constants (k yr^{-1}) ± SEM for each litter species. The color of the bars indicates the litter origin. n= 60 for each species, except n=58 for *Diplotropis* and n=59 for *Eperua, Fraxinus, Ilex, Fagus* and all *Alnus* species.

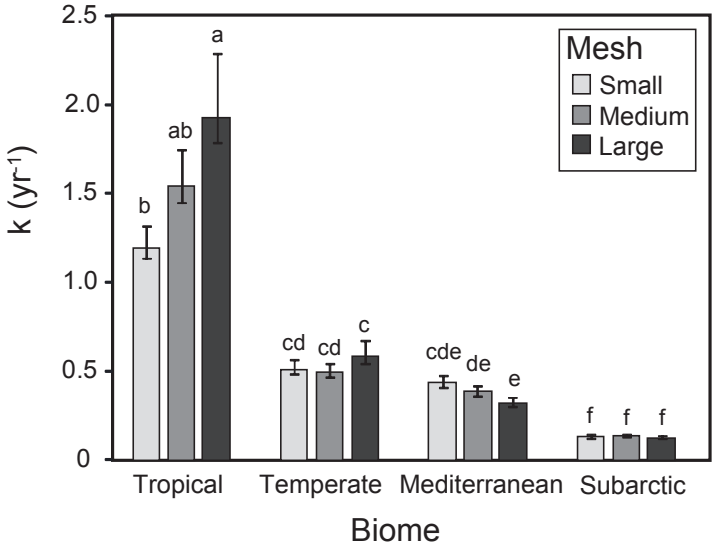

Figure S4.2. Average back-transformed decay rates (yr^{-1}) ± SEM for each mesh size treatment in each biome. n=80 except: n=77 for small mesh size in subarctic biome, n=78 for medium and large mesh sizes in the subarctic biome, and n=79 for small mesh size in tropical biome and large mesh in the temperate biome. Mesh size treatments are given by different tones of grey.

Appendix S5: Correlations between k and trait attributes

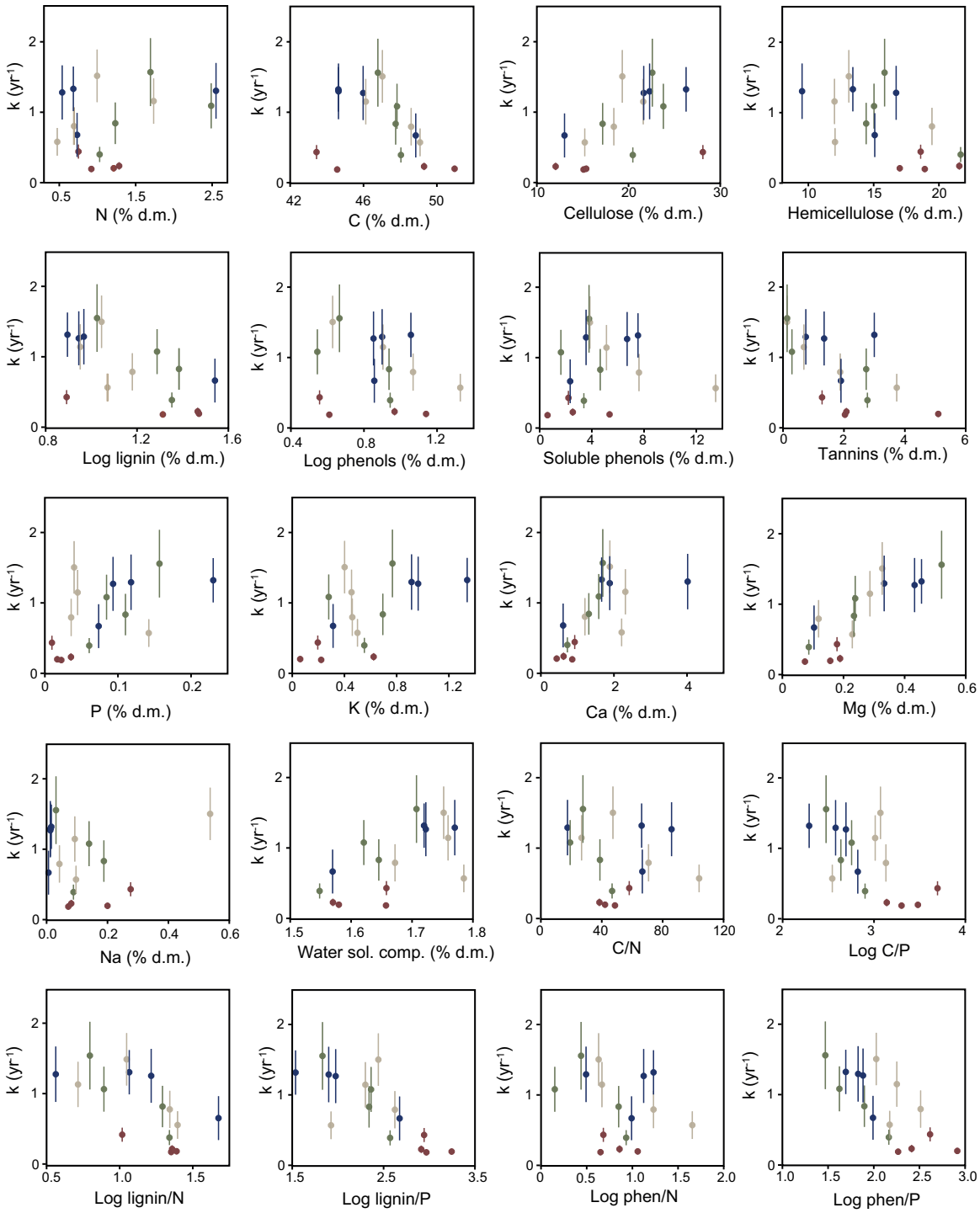

Figure S5. Continues on next page...

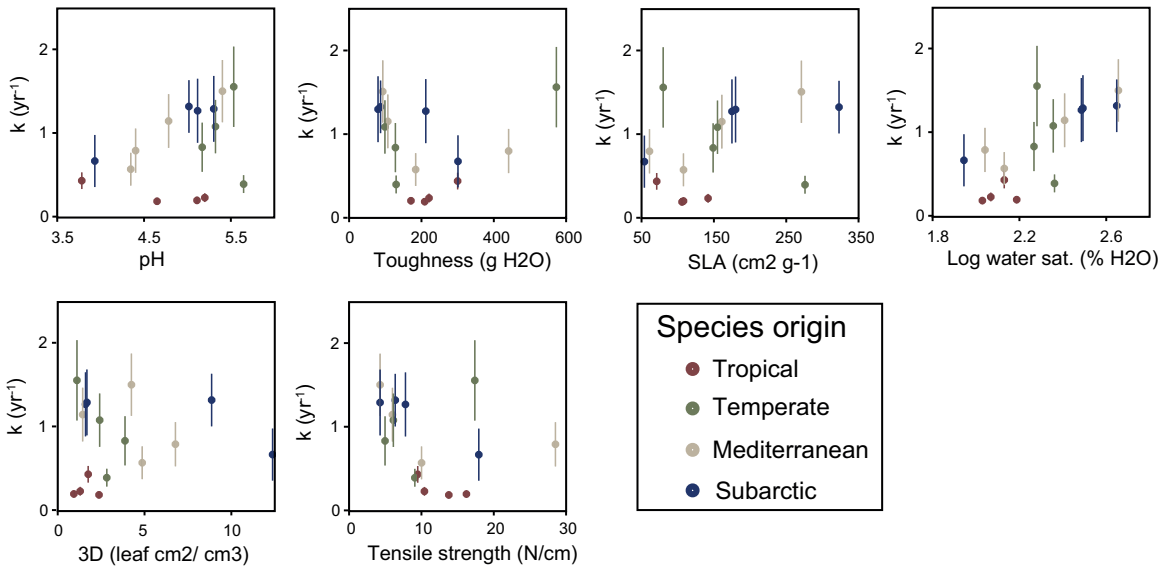

Figure S5. Correlation scatter plots for average decomposition rate constants (k yr^{-1}) ± SEM and the trait attribute per litter species for all chemical concentration, chemical ratios and physical traits. The average decomposition rate constants are calculated from 12 datasets (four biomes x three mesh sizes), thus n=12. Litter species are given in different colors according to their origin.