Plant litter functional diversity effects on litter mass loss depend on the macro-detritivore community

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ABSTRACT

A better understanding of the mechanisms driving litter diversity effects on decomposition is needed to predict how biodiversity losses affect this crucial ecosystem process. In a microcosm study, we investigated the effects of litter functional diversity and two major groups of soil macro-detritivores on the mass loss of tree leaf litter mixtures. Furthermore, we tested the effects of litter trait community means and dissimilarity on litter mass loss for seven traits relevant to decomposition. We expected macro-detritivore effects on litter mass loss to be most pronounced in litter mixtures of high functional diversity. We used 24 leaf mixtures differing in functional diversity, which were composed of litter from four species from a pool of 16 common European tree species. Earthworms, isopods, or a combination of both were added to each litter combination for two months. Litter mass loss was significantly higher in the presence of earthworms than in that of isopods, whereas no synergistic effects of macro-detritivore mixtures were found. The effect of functional diversity of the litter material was highest in the presence of both macro-detritivore groups, supporting the notion that litter diversity effects are most pronounced in the presence of different detritivore species. Species-specific litter mass loss was explained by nutrient content, secondary compound concentration, and structural components. Moreover, dissimilarity in N concentrations increased litter mass loss, probably because detritivores having access to nutritionally diverse food sources. Furthermore, strong competition between the two macro-detritivores for soil surface litter resulted in a decrease of survival of both macro-detritivores. These results show that the effects of litter functional diversity on decomposition are contingent upon the macro-detritivore community and composition. We conclude that the temporal dynamics of litter trait diversity effects and their interaction with detritivore diversity are key to advancing our understanding of litter mass loss in nature.

1. Introduction

Biodiversity is changing at an unprecedented rate across ecosystems (Maxwell et al., 2016; Millenium Ecosystem Assessment, 2005). This trend is particularly concerning, given mounting evidence that ecosystem functions depend on biodiversity (Balvanera et al., 2006; Cardinale et al., 2011; Hooper et al., 2012). Given their central role in ecosystem functioning, primary productivity and decomposition of dead organic matter have often been investigated in the literature as responses to changes in biodiversity (Cardinale et al., 2012, 2011;

Handa et al., 2014; Hooper et al., 2005). Processes of decomposition in particular involve a plethora of varied groups of organisms that have different functional roles and interact with each other to fragment organic material, degrade complex organic compounds, and mineralize nutrients (Coleman et al., 2004). By releasing compounds captured in dead organic matter, litter decomposition is crucial for carbon and nutrient cycling, and the maintenance of soil fertility, carbon storage, and ecosystem productivity (Hobbie, 1996; Wardle et al., 1997). In forests specifically, leaf litter is a major driver of soil processes by influencing soil pH and microbial communities (Ball et al., 2009;

Langenbruch et al., 2012; Reich et al., 2005). A loss of biodiversity at the level of primary producers, as well as within the diverse groups of microbial and animal decomposers is thus likely to alter decomposition, but its extend and functional consequences remain difficult to predict (Gartner and Cardon, 2004; Hättenschwiler, 2005).

Early studies of ecosystem functions focused on responses to plant species richness (Hooper et al., 2005). In accordance, many studies have manipulated litter diversity at the species level to test its relationship to decomposition rate (Handa et al., 2014; Hättenschwiler, 2005). Mixing litter from different plant species accelerates litter mass loss compared to single litter species in the majority of studies, although mixing has also been found to decelerate, or to have no effects on mass loss in other studies (Cardinale et al., 2006; Gartner and Cardon, 2004; Hättenschwiler, 2005). These inconsistent results might be caused by the complexity of the decomposition process (Gartner and Cardon, 2004), and discrepancies in results from previous studies may be due to how much of this complexity is incorporated into experimental designs. To date, interactions between two aspects of this complexity have not been adequately addressed: functional traits of litter mixtures and the composition and functional traits of the detritivore community.

Variation in species traits (i.e. functional traits) in a community drives ecosystem functions (Cornwell et al., 2008; Díaz et al., 2004; Loreau et al., 2002). Functional traits are morphological, biochemical, physiological, structural, phenological, or behavioural characteristics of organisms that influence performance or fitness (Garnier et al., 2015; Violle et al., 2007; see Nock et al., 2016 for introduction). A growing number of researchers are adopting trait-based approaches as they may facilitate the understanding of mechanisms and allow the transfer of findings among different locales and taxa (Dias et al., 2013; Kattge et al., 2011; Ricotta and Moretti, 2011; Violle et al., 2007). Trait information at the community level thus can help to predict the consequences of changes in community composition or biodiversity for focal ecosystem functions, such as decomposition (Díaz and Cabido, 2001; Luck et al., 2009; Mouillot et al., 2011; Suding et al., 2008). Litter quality (e.g. nutrient content, inhibitory secondary compounds, lignin content) is known to affect decomposition rate (i.e. litter mass loss) for many plant species (Aber et al., 1990; Coûteaux et al., 1995; Gholz et al., 2000). Numerous mechanisms given to explain the increased mass loss in litter mixtures involve trait complementarity: nutrient transfer among litter species, complementary resource use by consumers, and a more diverse physical environment for detritivore species (Gartner and Cardon, 2004; Gessner et al., 2010; Hättenschwiler, 2005). Based on trait information, a variety of functional diversity indices have been developed that reflect different aspects of biodiversity (Dias et al., 2013; Laliberte and Legendre, 2010; Schleuter et al., 2010) and test specific ecological hypotheses (Boersma et al., 2016). In comparison to species richness, functional diversity has been proposed as a better biodiversity metric that enhances the predictive capacity to explain ecosystem functions (Díaz and Cabido, 2001; McGill et al., 2006; Petchey and Gaston, 2006). The quantitative differences (physical, chemical) among taxa that are reflected in functional diversity play important roles in the process of decomposition (Heemsbergen et al., 2004). The influence of functional diversity on litter decomposition remains poorly understood, despite indications that it may help to understand the mechanisms underlying this process. Indeed, in the few studies to date, community-weighted means (mean trait value of a community, weighted by abundance) of litter traits and functional diversity have been found to be better predictors of decomposition compared to species richness (Aubert et al., 2010; Finerty et al., 2016).

Inconsistent results reported in studies to date of the diversity-decomposition relationship may also be due to inconsistent consideration of multi-trophic interactions, i.e. the differences in inclusion of different detritivores in the system. Decomposers play a central role in decomposition, but the different size classes (micro-organisms to macro-detritivores) and functional groups (e.g., fauna, bacteria, fungi) of organisms involved contribute differently to the breakdown and

mineralization of litter of different plant species (Bradford et al., 2002; Hättenschwiler, 2005; Hättenschwiler and Gasser, 2005). In addition to microflora (bacteria and fungi) that produce the majority of enzymes degrading complex organic compounds, the decomposition process is also strongly determined by the feeding activities of macro-detritivores (Cardinale et al., 2000; Hättenschwiler et al., 2005; Purahong et al., 2016; Srivastava et al., 2009). Terrestrial macro-detritivores encompass a remarkable diversity of litter- and soil-dwelling invertebrates (Coleman et al., 2004; Decaëns, 2010), which increase litter mass loss by breaking litter into smaller pieces, consuming it, and contributing to the proliferation of soil microorganisms (David and Handa, 2010; Hassall et al., 1987; Paoletti, 1999). Litter diversity effects on decomposition rates are largely attributed to the impact of litter on macro-detritivores through food selection and consumption rates (Cárcamo et al., 2000; Hättenschwiler and Bretscher, 2001; Hättenschwiler and Gasser, 2005). Thus, variations in traits due to changes in the litter composition may affect litter mass loss by altering its palatability for macro-detritivores and the physical properties (e.g. water retention) of the litter layer environment (de Bello et al., 2010; Makkonen et al., 2013). Synergistic effects have often been found between litter diversity and macro-fauna presence on litter mass loss, where litter loss in mixtures was higher than expected from monocultures, but only with the presence of macro-detritivores (Hättenschwiler and Gasser, 2005; Rouifed et al., 2010; Vos et al., 2011). The identity of macro-detritivores plays an important role in the way litter diversity affects litter mass loss as some detritivore species show stronger effects than others (Vos et al., 2011). Also, functionally different groups of macro-detritivores have been found to interact positively when removing soil surface litter (Heemsbergen et al., 2004).

Interactions between macro-detritivores and their effects on litter decomposition may be contingent upon litter quality and functional diversity. Numerous feeding trials, especially with earthworms, show that not all leaf types are equally well and rapidly decomposed (Hättenschwiler et al., 2005; Vos et al., 2011). Litter quality can greatly influence the feeding behaviour of macro-detritivores (Eisenhauer et al., 2009; Reich et al., 2005). Macro-detritivores will first feed on the most palatable available litter, and only consume litter of low nutritional value later when nothing else is available and once microorganisms have increased its palatability through their presence and the degradation of recalcitrant compounds like lignin (Paoletti, 1999; Vos et al., 2011). Litter with low carbon to nitrogen ratio (C:N) and high nutrient content (especially calcium, phosphorus, and magnesium) will be preferred in comparison to litter rich in defensive compounds (e.g. phenolics, tannins) or with a hard leaf structure and high lignin content (Cadish and Giller, 1997; Coûteaux et al., 1995; Dudgeon et al., 1990; Hättenschwiler and Bretscher, 2001; Hendriksen, 1990; Rajapaksha et al., 2013; Reich et al., 2005). In some cases, the ratio between nutrients (especially C:N and nitrogen to phosphorus ratio) are more important for palatability than the absolute content of those elements (Hättenschwiler, 2005). Especially the values of N and C:N have been used as highly relevant litter quality proxies (Aber et al., 1990; Cadish and Giller, 1997; Coûteaux et al., 1995; Gholz et al., 2000). Also, in mixed litter experiments, litter dissimilarity in nutrient content was found to increase litter mass loss as chemically different litter species complement each other to provide essential nutrients for macro-detritivores (Dudgeon et al., 1990; Vos et al., 2013). Considering how litter quality and diversity influence the effects of macro-detritivores on litter decomposition, the nature of interaction among macro-detritivore species may be contingent upon the functional diversity of litter species.

Earthworms and isopods are two of the main macro-detritivore groups found in forest ecosystems, account for a large part of the living biomass in soil, and contribute greatly to decomposition and nutrient mineralization (David and Handa, 2010; Hassall et al., 1987; Vos et al., 2011). While both functional groups fragment leaves into smaller particles, the feeding strategies differ between them. Earthworms tend to be soil-dwelling and pull leaf fragments belowground to feed on them,

while isopods reside in the litter layer to break down the litter. The two groups might also have different food preferences, which would increase their functional complementarity. As they share habitat and food source, direct and indirect interactions between these two invertebrate groups can be expected to influence decomposition dynamics. However, how interactions between earthworms and isopods affect litter mass loss has rarely been studied. On the one hand, positive interactions between earthworms and isopods can be expected if they differ in resource use and earthworms fragment litter in a way that is better accessible for isopods. On the other hand, they might compete for litter material as a food source and thus negatively interact, particularly if the availability of high quality litter is limited (Zimmer et al., 2005).

In this study, we tested how tree litter functional diversity influences the performance of two interacting macro-detritivores (isopods and earthworms) on soil surface litter mass loss. We explored the role of litter traits and functional diversity calculated from seven decomposition-related litter traits (Laliberte and Legendre, 2010). Given the important role of macro-detritivores, we expect that the presence of each of these macro-detritivore groups will enhance litter mass loss (Hättenschwiler et al., 2005). More specifically, we hypothesize 1a) that the rate of surface litter mass loss is highest in the presence of both macro-detritivore groups, if resource use complementarity is more important than competition (De Oliveira et al., 2010; Hättenschwiler and Jørgensen, 2010; Schädler and Brandl, 2005; Zimmer et al., 2005). Alternatively, we hypothesize (1b) that litter mass loss in the presence of the two macro-detritivore groups will be less than additive if the two groups compete strongly. Furthermore, we hypothesize 2) that a high tree litter functional diversity based on decomposition-relevant litter traits would lead to resource partitioning between the two macro-detritivore species used in this study, resulting in increased consumption efficiency and reduced competition between the two macro-detritivore species when mixed (Hättenschwiler and Gasser, 2005; Hillebrand et al., 2008). Finally, we hypothesize 3) that litter mass loss is regulated by the community mean of certain decomposition-relevant litter traits (e.g. concentration of phenolics and tannins), but the dissimilarity of others, especially N content ratio (Vos et al., 2013).

2. Methods

2.1. Litter mixtures

This experiment used litter collected from the field site "Bechstedt" (50°54′N, 11°05′E, Germany, altitude = 408 m asl), that is part of the BIOTREE project (Scherer-Lorenzen et al., 2007b) and a global network of tree diversity experiments (TreeDivNet; Verheyen et al., 2016). In 2003, the BIOTREE-FD tree diversity experiment was established from a pool of 16 common European species (*Acer campestre* L., *Acer platanoides* L., *Acer pseudoplatanus* L., *Betula pendula* Roth, *Carpinus betulus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Larix decidua* Mill., *Pinus sylvestris* L., *Populus tremula* L., *Prunus avium* L., *Quercus petraea* Liebl., *Sorbus aucuparia* L., *Sorbus torminalis* (L.) Crantz, *Tilia cordata* Mill., and *Ulmus glabra* Huds.) to test the effects of tree functional diversity on ecosystem processes. Within each plot for a total of 24 plots (mixtures), species richness was held constant at four species, relative abundance was equal for all species, and only the functional diversity of the mixture was varied. Functional diversity was determined using nine relevant structural and physiological above- and below-ground tree traits. Trees were planted as small monospecific patches within each plot to prevent competitive exclusion of species with slow juvenile growth rates (e.g. *F. sylvatica*) by species with fast juvenile growth rates (e.g. *P. tremula*). Not all tree species from the 16 species pool were present in the same number of plots (Table 1). In the litter decomposition experiment presented here, we used litter mixtures corresponding to the BIOTREE-FD mixtures (Scherer-Lorenzen et al., 2007b).

2.2. Sampling of litter, soil, and animals

Recently abscised leaves of all species, except *C. betulus*, *F. sylvatica*, and *Q. petraea* were collected in November 2012. Litter material of the remaining three tree species, for which leaf abscission is mostly incomplete until spring, was collected in April 2013. All litter material was air-dried. Soil for the microcosms was collected from the Bechstedt site (soil pH = 6.8, nitrogen content = 0.3%, carbon content = 2.7%, C:N ratio = 10.9; Scherer-Lorenzen et al., 2007) and mixed in a ratio of 1:1 with soil from the Jena Experiment (50°57′N, 11°37′E, altitude = 130 m asl, soil pH = 8.1, nitrogen content = 0.3%, carbon content = 4.6%, C:N ratio = 15.7; Eisenhauer et al., 2011), due to the high clay and stone content of the soil from Bechstedt.

We selected earthworms (*Lumbricus terrestris* L.) and terrestrial isopods (Isopoda; four species, details below) from the macro-detritivore community as they represent the two most important groups at the Bechstedt site (G. Patoine, unpublished data). *L. terrestris* is an anecic earthworm species forming vertical burrows, which contribute to soil building processes, bioturbation, and the mineralization of nutrients (Edwards, 2004). By pulling litter material into the top part of their semi-permanent burrows and mixing it with faeces, they typically improve nutrient availability for plants and alter the number and species composition of other soil organisms (Eisenhauer, 2010). Earthworms were purchased from a local supplier (Natursache, Germany) and kept in the study soil mixture for 10 days to acclimate to the experimental conditions (Fründ et al., 2009).

Terrestrial isopods (Isopoda) generally inhabit deadwood or the soil surface litter layer. Despite their relatively small body size compared to earthworms, they play an important role in the decomposition of leaf litter and dead wood through the mineralization and humification of organic matter. Individuals of four species of isopods (*Porcellio scaber* (Latreille), *Oniscus asellus* L., *Philoscia muscorum* (Scopoli), and *Armadillidium vulgare* (Latreille)) were collected at the edge of the field site of the Jena Experiment (Roscher et al., 2004) and resembled the species present at Bechstedt.

2.3. Experimental setup

Microcosms were constructed from PVC pipes (40 cm in height, 12 cm in diameter) closed with a 50 μm nylon mesh at the base and a lid on top with a 2 cm diameter hole in the middle. Each microcosm was half-filled with sieved soil (4 mm) that was defaunated by drying at 60 °C for three days, and then watered with 400 ml of distilled water per microcosm to leach nutrients that were released during the defaunation procedure (Alphei and Scheu, 1993). Plot-specific litter (4 g in total, 1 g per species) was added after three days, reproducing the 24 BIOTREE-FD mixtures (Scherer-Lorenzen et al., 2007b) with four replicates each. After another 14 days, the macro-detritivores were added to establish four treatments: (1) Nine isopods (0.21 ± 0.01 g mean and standard error of total fresh weight), (2) one earthworm (3.4 ± 0.2 g), (3) nine isopods and one earthworm (later referred to as mixed treatment), and (4) control without macro-detritivores, resulting in a total of 96 microcosms (24 × 4). The number of macro-detritivore used were within the range of densities found under natural field conditions (Jabin et al., 2004; Paoletti, 1999; Paoletti and Hassall, 1999; Schwarz et al., 2015). The four isopod species were equally distributed across the microcosms. All animals were weighed before being added to the microcosms in order to assess weight changes over the experimental period. According to previous studies, we did not use a substitutive design because of the large body mass differences between earthworms and isopods (e.g. Heemsbergen et al., 2004); however, initial differences in total macro-detritivore biomass should be considered when interpreting the results. The microcosms were placed randomly inside a climate chamber with a day/night cycle and temperatures of 20 °C during daytime (16 h) and 15 °C during the night (8 h). The temperature changes took place over a period of three hours in the morning and

Table 1

Species mixtures of the BIOTREE-FD experiment in Bechstedt, Germany, ordered by the functional dispersion index of decomposition-relevant traits used in this study. Plot numbers refer to the field site.

	Plot	Species 1	Species 2	Species 3	Species 4
Increasing functional diversity ↑	1	A. pseudoplatanus	B. pendula	P. sylvestris	S. torminalis
	20	C. betulus	P. sylvestris	Q. petraea	F. excelsior
	4	A. campestre	F. excelsior	P. sylvestris	P. tremula
	15	B. pendula	P. sylvestris	P. tremula	P. avium
	5	A. pseudoplatanus	C. betulus	L. decidua	P. avium
	22	A. campestre	F. excelsior	L. decidua	T. cordata
	11	A. platanoides	A. pseudoplatanus	P. tremula	S. aucuparia
	23	B. pendula	C. betulus	L. decidua	U. glabra
	8	A. campestre	A. platanoides	F. excelsior	T. cordata
	12	A. platanoides	C. betulus	T. cordata	U. glabra
	16	A. platanoides	C. betulus	P. tremula	U. glabra
	24	C. betulus	F. excelsior	S. aucuparia	S. torminalis
	18	B. pendula	L. decidua	Q. petraea	S. torminalis
	21	A. platanoides	A. pseudoplatanus	B. pendula	Q. petraea
	17	B. pendula	C. betulus	P. avium	T. cordata
	3	A. platanoides	Q. petraea	T. cordata	U. glabra
	6	A. campestre	A. platanoides	A. pseudoplatanus	S. aucuparia
	14	Q. petraea	S. aucuparia	T. cordata	U. glabra
	9	A. campestre	S. aucuparia	S. torminalis	U. glabra
	7	A. platanoides	F. excelsior	P. avium	S. torminalis
	10	A. platanoides	F sylvatica	S. aucuparia	U. glabra
	19	P. tremula	P. avium	S. aucuparia	S. torminalis
	2	B. pendula	F sylvatica	Q. petraea	U. glabra
	13	B. pendula	F sylvatica	S. aucuparia	S. torminalis

evening. The experiment ran over a period of 8 weeks, in which the loss of soil surface litter coverage was visually estimated twice a week by considering the percentage of soil covered with litter when looking from the top. During the last four weeks of the experiment, 10 ml of distilled water was added per microcosm per week.

After 8 weeks, litter cover was estimated again, and the remaining litter was collected and separated by tree species, dried (60 °C for 3 days), and weighed. Unidentified litter material accounted on average for 1.7% of the total litter mass remaining. The final weight of the species-specific litter was higher than initial weight (1 g) in 24 cases (out of 384), possibly due to attached fecal pellets or fungal growth during the experiment, despite the cleaning of the leaves. The macro-detritivores were collected, weighed, and then frozen. Individuals that could not be found at the end of the experiment were assumed to have died, as escape was not possible. Juvenile isopods were counted and weighed. Three soil cores (2.5 cm diameter, 5 cm depth) were taken from each microcosm at the end of the experiment and pooled for analysis of soil water content. Earthworm response was quantified by the survival rate and weight change (log (final weight/initial weight)), while isopod response was quantified by survival rate and reproductive success (number of juveniles). The total weight change of isopods was also measured but was not used, as it correlated well with the survival rate ($r = 0.76$, $p < 0.001$). Earthworms were missing in five microcosms. Analysis of the change of litter cover over time indicated that they most likely died during the first half of the experiment. Data from these five microcosms were therefore only considered for the earthworm survival response and were not considered for other analyses like litter mass loss.

2.4. Traits and functional diversity

Decomposition-relevant traits were used to assess the effect of

functional diversity and specific traits on litter mass loss and macro-detritivore performance. The trait values are based on measurements by Hantsch et al. (2014) from fresh leaves sampled from five healthy randomly selected individuals on different plots at the Bechstedt site. The respective data are therefore specific to this site. The traits measured were: polyphenolic concentration (mg/g), tannin concentration (mg/g), N concentration (%), C:N ratio, leaf thickness (mm), leaf toughness (N), and specific leaf area (SLA; $cm^2 g^{-1}$) (see Hantsch et al. (2014) for details on measurement procedures). Leaf type was added as a factorial trait (coniferous or broadleaf) for the calculation of functional diversity. Significant correlations were found among some of the traits (Table 2). Functional dispersion (Laliberte and Legendre, 2010) and functional richness (Villéger et al., 2008) are the two functional diversity indices that we chose as they perform well and are commonly used (Boersma et al., 2016). They were calculated for each litter mixture using all traits except for N concentration, as it was already included in litter C:N ratio. Seven traits (phenolics, tannins, N concentration, C:N, leaf thickness, leaf toughness, and SLA) were also considered separately using the community weighted mean (weighing in this case did not affect the values as the litter species were in equal proportions; Ricotta and Moretti, 2011) and mean absolute deviation (MAD) of single traits separately. The MAD is also referred to as the average distance from the mean and is equivalent to the functional dispersion of a single trait, describing dissimilarity among species for a given trait (Laliberte and Legendre, 2010). The functional diversity indices were calculated using R software version 3.3.2 (R development Core Team) and the package 'FD' (Laliberte and Legendre, 2010).

2.5. Statistical analyses

Prior to analysis, litter cover data was arcsine-transformed. Pearson's correlations were used to create a correlation matrix of the

Table 2

Pearson's correlations of the tree leaf traits used in the present study. Trait measurements are based on Hantsch et al. (2014) from leaves of the Bechstedt BIOTREE-FD experiment (Scherer-Lorenzen et al., 2007b).

	Leaf type (coniferous species)	Phenols	Tannins	N	C:N	Leaf thickness	Leaf thickness WP[a]	Leaf toughness	Leaf toughness WP[a]
Phenols	−0.28								
Tannins	−0.26	0.94***							
N	0.29	−0.33	−0.29						
C:N	−0.20	0.33	0.25	−0.94***					
Leaf thickness	0.64**	−0.31	−0.20	−0.19	0.15				
Leaf thickness WP[a]	−0.16	−0.19	0.05	0.04	−0.03	NA			
Leaf toughness	0.56*	−0.17	−0.09	−0.36	0.30	0.92***	0.08		
Leaf toughness WP[a]	−0.35	0.30	0.36	−0.56*	0.47	0.08	0.08	NA	
Specific leaf area	−0.10	0.10	0.09	0.39	−0.40	−0.39	−0.01	−0.58*	−0.68**

Significance level is indicated for p < 0.05 (*), p < 0.01 (**) and p < 0.001 (***).

[a] WP indicates correlations without *Pinus* (see Section 'Species-specific litter mass loss' for details).

litter functional traits. A Pearson's correlation was also used to determinate the correlation between visually estimated litter cover removed and the weighed litter mass loss at the end of the experiment. For all models, we selected the most parsimonious model using Akaike's information criterion, corrected for small sample sizes (AICc; Burnham and Anderson, 2002). Effects of earthworm presence, isopod presence, experiment duration, functional dispersion, and all interactions on litter cover removed were tested using a general linear model (LM). Time series were also analyzed for each date excluding the duration variable to test the effect of functional dispersion and macro-detritivore treatments for each time point. Tukey's HSD tests were then used for pairwise comparison of the litter cover removed among the macro-detritivore treatments for each time point. To test the effects of each functional trait on litter mass loss (Eisenhauer et al., 2010), we analyzed the effects of each functional trait parameter separately, with all possible interactions with earthworm and isopod presence on litter mass loss. The functional trait parameters tested were functional dispersion, functional richness, and trait community means and MADs for seven traits (polyphenolics, tannins, N content, C:N, leaf toughness, leaf thickness, and SLA). Since functional dispersion and functional richness had qualitatively similar effects on litter mass loss and macro-detritivore performance, only results based on functional dispersion are presented here. Similarly, the effect of soil water content on litter mass loss was tested. We also tested the effects of the macro-detritivores on soil water content. The effects of earthworm and isopod initial weight on litter mass loss were tested in interaction with the presence of the other macro-detritivore groups.

The effects of species-specific litter mass loss were tested in LMs for each species as affected by earthworm presence, isopod presence, and their interaction. Tukey's HSD tests were used for pairwise comparisons among macro-detritivore treatments. Linear mixed-effects models were used to test the effects of earthworm presence, isopod presence, a functional trait, and all interactions with microcosm as a random intercept (as data on multiple litter species per microcosm entered the analyses) on species-specific litter mass loss. The variance explained by microcosm as a random intercept was always negligible. Further, when we compared the model fits between LMs (without random intercept) and linear mixed-effects model using AICc values, LMs always performed better (lower AICc values). Hence, we continued using LMs as our main statistical model.

Earthworm survival and weight change, and isopod survival and reproduction were tested against functional dispersion and trait community means and MADs of the seven litter traits in interaction with the presence of the other macro-detritivore group (e.g. the effects of earthworm presence, functional dispersion and their interaction on isopod survival). The responses of earthworm weight change and isopod survival were tested using LMs. For earthworm survival and isopod reproduction, generalized linear models (GLMS) were fitted with a binomial and a Poisson family respectively.

The linearity assumptions for all LMs were met (that is, there was no

correlation between the residual and fitted values). All statistical analyses were performed using R software version 3.3.2 (R development Core Team). Mixed-effect models were run with the "lme4" package (Bates et al., 2015). The significance threshold for all statistical models was set at 0.05.

3. Results

3.1. Litter cover

The estimated litter cover at the end of the experiment was strongly and significantly correlated to the dry weight of the leftover litter (r = 0.96, p < 0.001, Fig. 1a), indicating that the visual cover estimations during the experiment are a useful indicator of litter mass loss. The visually estimated litter cover decreased over time in all of the macro-detritivore treatments (Fig. 1b), while there was no change of litter cover in the control without macro-detritivores. The litter cover was significantly reduced after 13 days in the earthworm and mixed (with earthworm and isopods) treatments, and after 20 days in the isopod treatment (Fig. 1b). After the first week and for the rest of the experiment, we found no significant differences in cover between the earthworm and mixed treatments.

We found three significant three-way interactions in the model testing how litter cover loss was influenced by earthworm presence, isopod presence, experimental duration, functional dispersion of the litter traits, and all interactions (Table 3). Increasing functional dispersion reduced the litter cover loss in the isopod treatment, had a weak negative effect in the earthworm treatment, and increased the litter cover loss in the mixed treatment (Fig. 2a). From day 16 to day 34 of the experiment, a significant three-way interaction between functional dispersion, earthworm presence, and isopod presence was found (Fig. A1). During that period, litter cover loss was negatively influenced by functional dispersion in the isopod and earthworm treatments, but was positively influenced in the mixed treatment. Towards the end of the experiment, the effect of functional dispersion weakened (Fig. A1). However, overall functional dispersion increased litter cover loss more over time in treatments including earthworms (Fig. 2c).

3.2. Litter mass loss

Litter mass loss in the control, isopod, earthworm, and mixed treatments (in percent, mean ± SE) was 7.86 ± 0.70%, 29.62 ± 1.57%, 70.07 ± 2.99%, and 75.98 ± 3.64%, respectively, at the end of the experiment (Fig. 1c, Table 4). The final weight of the litter was significantly reduced in the presence of earthworms and isopods and was influenced by the interaction of the two macro-detritivores. While litter mass loss in the treatments with one macro-detritivore group was significantly increased, the combined effect of the macro-detritivores was less than their additive effects. Functional dispersion of the litter had no significant effect on litter mass loss
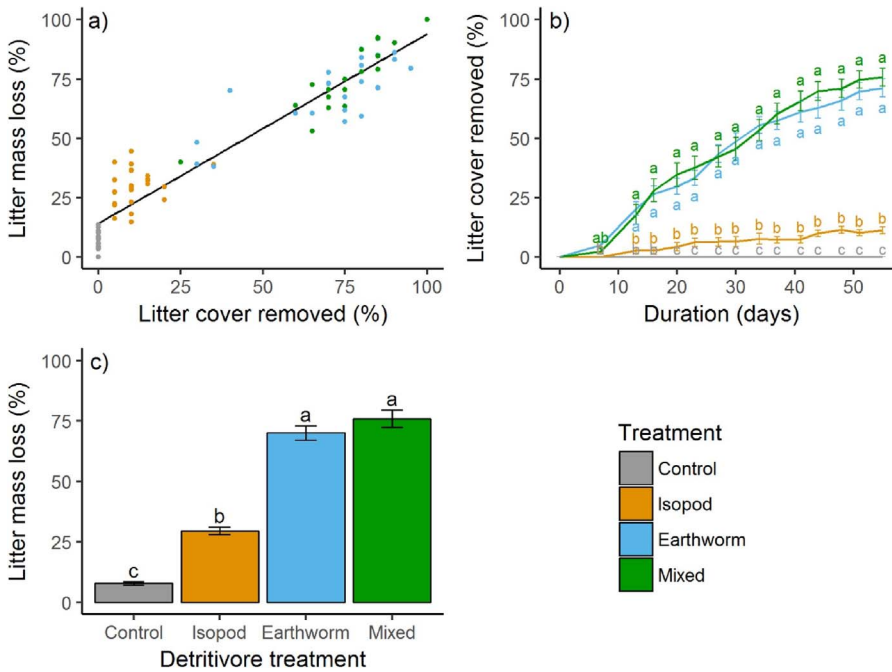
Fig. 1. a) Correlation between visually estimated litter cover removed and the weighed litter mass loss at the end of the experiment (r = 0.96, p < 0.001). b) Visually estimated litter cover (means ± standard error) removed in the different macro-detritivore treatments over the duration of the experiment. c) Effect of the macro-detritivore treatments on percentage litter mass loss (means ± standard error; Table 2). Different letters indicate significant differences among treatments at the specific dates (Tukey's HSD test). The mixed treatment included both earthworms and isopods.

Table 3

General linear model results of effects of earthworm presence, isopod presence, duration of the experiment, functional dispersion of litter traits, and interactions on visually estimated litter cover (arcsine). These results are based on the best-fit model (based on AICc values) reduced from a full model including all interactions. AICc full model = −551.2, AICc best model = −553.9. Residual dfs = 1351.

Factors	F	p
Earthworm presence (E)	5226.7	**< 0.001**
Isopod presence (I)	195.9	**< 0.001**
Duration (D)	1586.5	**< 0.001**
Functional dispersion (F)	0.2	0.664
E × I	140.2	**< 0.001**
E × D	761.1	**< 0.001**
I × D	74.5	**< 0.001**
E × F	23.0	**< 0.001**
I × F	1.4	0.241
D × F	6.3	**0.012**
E × I × D	33.3	**< 0.001**
E × I × F	30.8	**< 0.001**
E × D × F	5.0	**0.025**

Significant effects (p < 0.05) are highlighted in bold.

(p > 0.05). There was no difference of soil water content among macro-detritivore treatments (p > 0.05), and there was only a weak overall increase of litter mass loss with soil water content ($F_{1,78}$ = 4.4, p = 0.040) with no interaction with the macro-detritivore treatments.

Overall, none of the seven trait community means significantly affected litter mass loss across the macro-detritivore treatments (all p > 0.05). In contrast, the MAD of C:N ratio significantly increased litter mass loss (Fig. 2b; Table 4). None of the MADs of the other six traits influenced litter mass loss (all p > 0.05). Litter mass loss was increased by earthworm initial weights ($F_{1,41}$ = 6.4, p = 0.015) and final weights ($F_{1,41}$ = 11.7, p = 0.001, Fig. 3a). Isopod initial weights, final weights, and survival did not significantly influence litter mass loss (all p > 0.05).

3.3. Species-specific litter mass loss

The final weight of the species-specific litter was higher than initial weight (1 g) in 24 cases (out of 384), possibly due to attached fecal pellets and of fungal growth during the experiment, despite the

cleaning of the leaves. Macro-detritivore effects depended on litter identity (Fig. 4; Table 5). Overall, litter mass loss was highest for *Fraxinus excelsior* (69.8%), *Sorbus aucuparia* (68.7%), *Betula pendula* (63.4%), and *Prunus avium* (61.25%), and lowest for *Fagus sylvatica* (8.0%), *Quercus petraea* (12.0%), and *Sorbus torminalis* (23.8%). *Quercus petraea* was the only tree species with no significant effect of macro-detritivores on litter mass loss. For all species besides *F. sylvatica* and *Q. petraea*, litter mass loss was highest in the earthworm and mixed treatments, which did not differ significantly from each other. For *B. pendula*, *Carpinus betulus*, *F. excelsior*, *P. avium*, *S. aucuparia*, and *Ulmus glabra*, a similar pattern was observed as with the total litter mixture. For those species, there was a significantly lower litter mass loss in the isopod treatment than in both the earthworm and mixed treatments, but it was significantly higher than in the control. In five other species (*Acer campestre*, *Acer platanoides*, *Acer pseudoplatanus*, *Populus tremula*, and *Tilia cordata*), litter mass loss was significantly higher in the mixed and earthworm treatments than in the isopod and control treatments, which did not differ significantly from each other. For the remaining five species (*F. sylvatica*, *Larix decidua*, *Pinus sylvestris*, *Q. petraea*, and *S. torminalis*), litter mass loss in the control and/or the isopod treatment was not significantly different from that of the earthworm and/or mixed treatment. Litter mass loss was significantly higher only for six tree species (*B. pendula*, *C. betulus*, *F. excelsior*, *P. avium*, *S. aucuparia*, and *U. glabra*) in the isopod treatment than in the control. For eight species (*B. pendula*, *C. betulus*, *F. excelsior*, *P. tremula*, *P. avium*, *S. aucuparia*, *T. cordata*, and *U. glabra*), litter mass loss was higher than 90% in at least one of the treatments including earthworms.

Analysis for leaf toughness and leaf thickness were performed with and without *P. sylvestris* in order to test the influence of the high leverage of that species (exceptionally high values for leaf toughness and thickness compared to the other species). Litter mass loss decreased significantly with increasing polyphenolic content (Fig. 5a, Table 6), tannin content (Fig. 5b, Table 6), and leaf toughness with (Fig. 5e, Table 6) and without *P. sylvestris* (Fig. 5f, Table 6), whereas it increased significantly with increasing N content (Fig. 5c, Table 6) and leaf thickness without *P. sylvestris* (Fig. 5d, Table 6) of the litter material across the macro-detritivore treatments. By contrast, the relationship between specific leaf area and litter mass loss differed among the macro-detritivore treatments (Fig. 5g, Table 6). While specific leaf area had a positive relationship with litter mass loss in the earthworm and
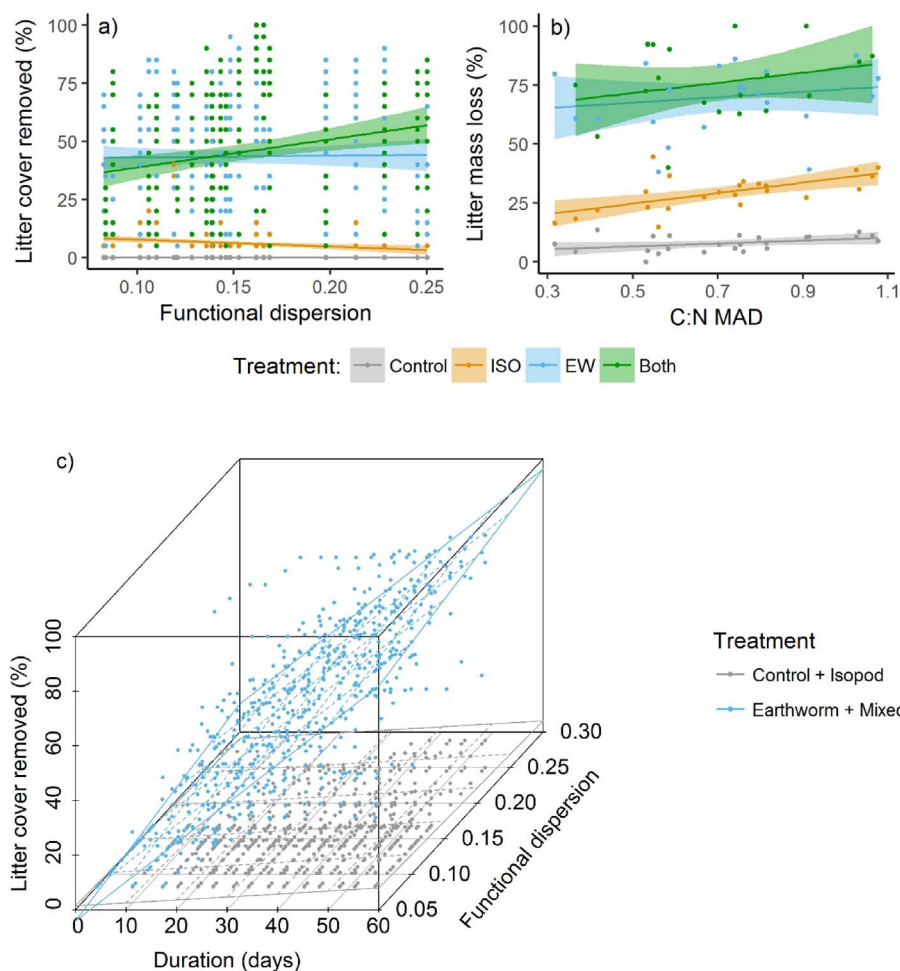
Fig. 2. a) Functional dispersion of litter traits influence on soil surface litter cover removed over the duration of the experiment (Table 1). b) C:N mean absolute deviation (MAD) influence on percentage litter mass. Lines in figure a and b are based on linear regressions (LM) with 95% confidence intervals (Table 2). c) Temporal increase of litter cover removed as influenced by functional dispersion of litter traits over the experimental period (Table 1).

Table 4
General linear model results of effects of earthworm presence, isopod presence, and interactions, as well as with C:N MAD and interactions on litter mass loss. These results are based on the best-fit model (based on AICc values) reduced from a full model including all interactions.

Factors	Residual dfs	Full model AICc	Best model AICc	F	p
Only detritivore treatment	87	706.1	706.1		
Earthworm presence (E)				531.7	< 0.001
Isopod presence (I)				36.4	< 0.001
E × I				11.1	0.001
with C:N MAD	86	706.6	701.1		
E				572.1	< 0.001
I				39.7	< 0.001
MAD of C:N				7.2	0.009
E × I				11.4	0.001

Significant effects (p < 0.05) are highlighted in bold.

mixed treatments, litter mass loss decreased with increasing specific leaf area in the presence of isopods. The C:N ratio and leaf thickness including *P. sylvestris* had no significant effects on litter mass loss.

3.4. Performance of macro-detritivores

Earthworm survival and weight change, as well as isopod survival and reproduction, were not influenced by any of the functional traits of tree litter (functional dispersion, litter trait community means and MADs; all p > 0.05), nor by soil water content (p > 0.05).

Earthworm survival was significantly reduced in the presence of isopods (-21%; $F_{1,46} = 14.4$, p < 0.001; Fig. 6a). By contrast, earthworm initial weight and isopod initial weight, final weight, and survival had no significant effect on earthworm survival. Earthworm final weight was strongly and only driven by initial weight ($F_{1,41} = 185.7$, p < 0.001). Earthworm weight (initial and final) was negatively related to the weight change of earthworms (Fig. 3b). This means that larger earthworms lost weight or maintained their weight, while smaller earthworms gained more weight during the experiment. Isopod presence did not affect the log response ratio of earthworm weight (p > 0.05).

Isopod survival was significantly reduced in the presence of earthworms (-16%; $F_{1,41} = 5.4$, p = 0.025; Fig. 6b), but was not significantly influenced by the body weight of earthworms and isopods. In addition, the number of juvenile isopods was strongly reduced by the presence of earthworms ($F_{1,41} = 42.8$, p < 0.001; Fig. 6c).

4. Discussion

4.1. Macro-detritivore treatments

The results of our study show that the presence of isopods and earthworms drove overall litter mass loss, with a less than additive effect when both detritivore groups were present. Earthworms had a stronger effect on litter mass loss than isopods, highlighting the findings of earlier studies on the role of detritivore identity effects on litter mass loss (Hättenschwiler and Gasser, 2005; Heemsbergen et al., 2004; Vos et al., 2011). In the study by Zimmer et al. (2005), although litter mass loss was always higher with the presence of earthworms and isopods
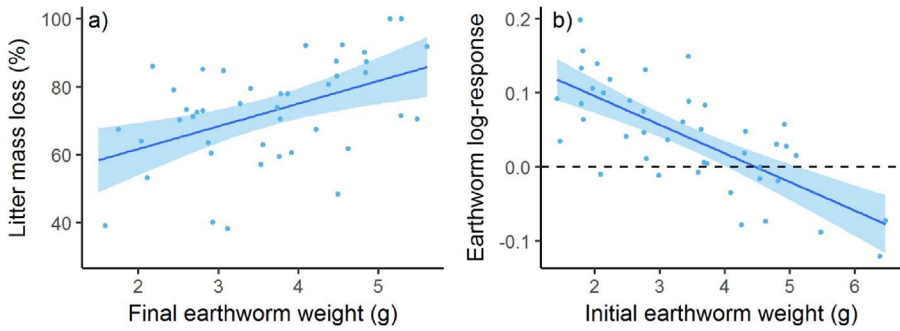
Fig. 3. a) Final earthworm weight influence on percentage litter mass loss in the earthworm and mixed treatments on litter mass loss ($F_{1,41} = 11.7$, $p = 0.001$). b) Initial earthworm weight influence on earthworm weight change (log (body weight at the end of the experiment/initial body weight)) in the earthworm and mixed treatments ($F_{1,41} = 185.7$, $p < 0.001$). All the lines in the figure above are based on linear regressions (LM) with 95% confidence intervals.
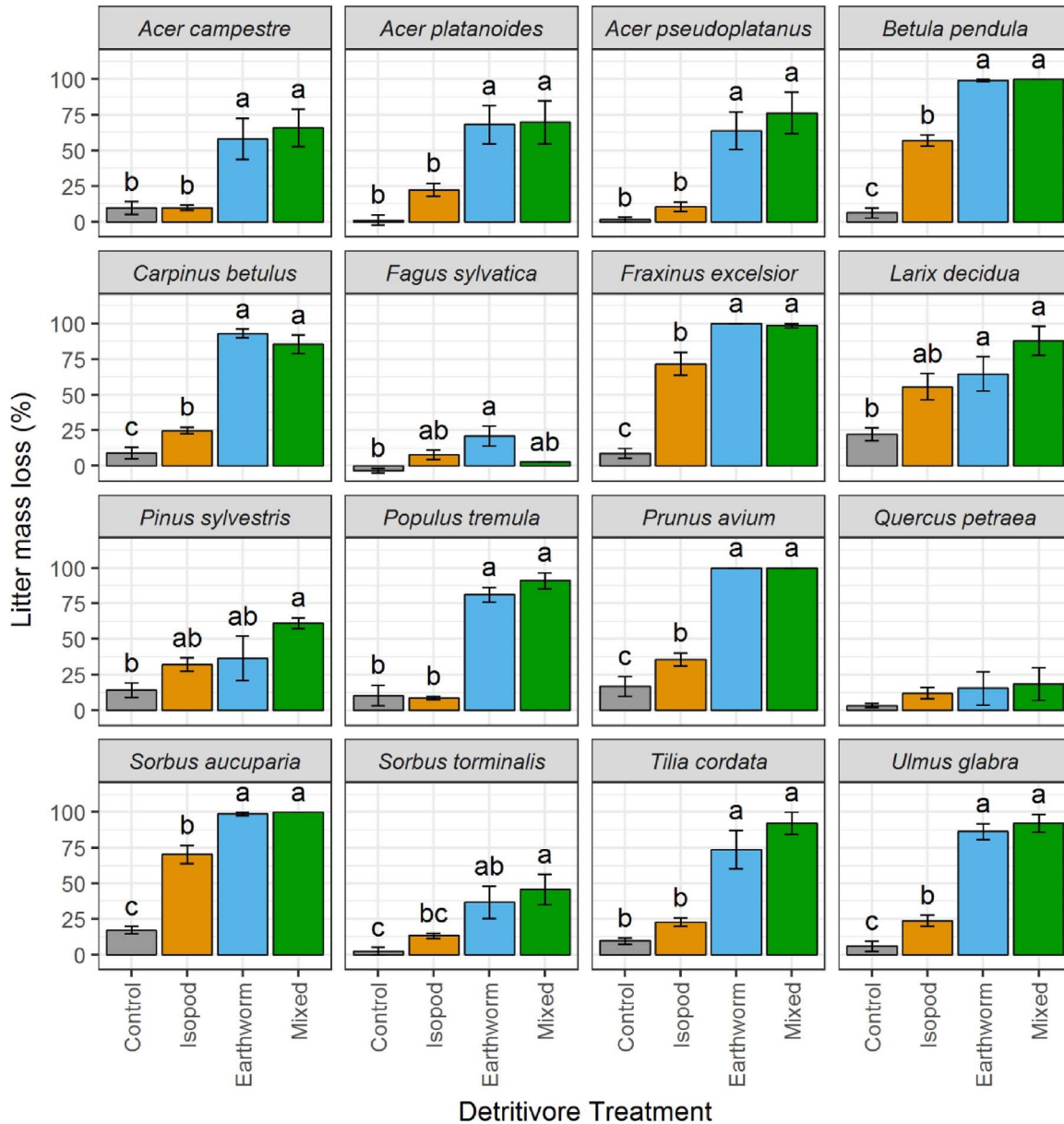

Fig. 4. Tree species-specific litter mass loss (means ± standard error) for each macro-detritivore treatment (Table 4). Means with standard error. Different letters indicate significant differences among the macro-detritivore treatments (Tukey's HSD test).

together than with a single macro-detritivore, the effects with both macro-detritivores were still less than additive with mixed litter. The authors of this study suggest that the negative non-additive effects of detritivores may be caused by functional redundancy of detritivores or because detritivore biomass might saturate the decomposition processes.

4.2. Functional diversity

The macro-detritivore community determined the effect of litter

Table 5
General linear model results of effects of earthworm presence, isopod presence, and interaction on species-specific litter mass loss.

Species	n	Earthworm presence (E)		Isopod presence (I)		E × I	
		F	p	F	p	F	p
A. campestre	20	26.9	**< 0.001**	0.2	0.699	0.1	0.716
A. platanoides	34	34.9	**< 0.001**	1.5	0.228	1.0	0.327
A. pseudoplatanus	20	41.7	**< 0.001**	1.2	0.297	0.0	0.874
B. pendula	30	613.9	**< 0.001**	96.8	**< 0.001**	78.3	**< 0.001**
C. betulus	27	318.0	**< 0.001**	1.2	0.279	8.2	**0.009**
F. sylvatica	10	7.5	**0.034**	0.1	0.798	6.8	**0.041**
F. excelsior	24	174.6	**< 0.001**	47.5	**< 0.001**	51.9	**< 0.001**
L. decidua	16	15.8	**0.002**	9.1	**0.011**	0.3	0.596
P. sylvestris	15	7.5	**0.020**	5.1	**0.045**	0.1	0.724
P. tremula	19	207.3	**< 0.001**	0.5	0.494	1.2	0.290
P. avium	19	273.8	**< 0.001**	5.0	**0.041**	4.4	0.053
Q. petraea	21	1.4	0.259	0.5	0.470	0.1	0.737
S. aucuparia	29	225.5	**< 0.001**	60.5	**< 0.001**	43.0	**< 0.001**
S. torminalis	27	18.7	**< 0.001**	1.7	0.208	0.0	0.918
T. cordata	22	64.7	**< 0.001**	3.6	0.074	0.1	0.757
U. glabra	29	247.9	**< 0.001**	7.1	**0.014**	1.5	0.229

Significant effects (p < 0.05) are highlighted in bold.
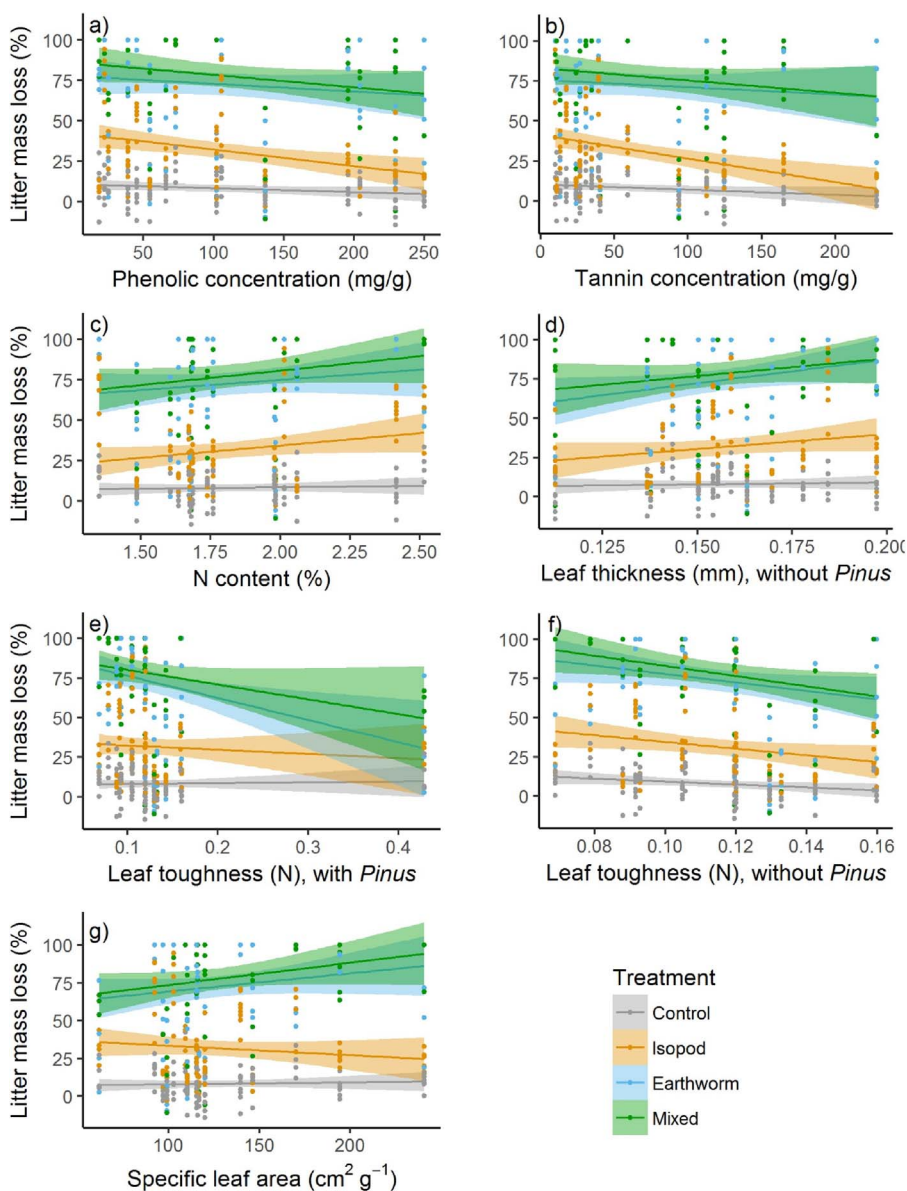
Fig. 5. Relationships between species-specific litter mass loss and the litter traits a) phenolic concentration, b) tannin concentration, c) nitrogen content, d) leaf thickness, excluding *P. sylvestris* litter, e) leaf toughness, including *P. sylvestris* litter, f) leaf toughness, excluding *P. sylvestris* litter, and g) specific leaf area in the different macro-detritivore treatments (Table 5). Leaf thickness including *P. sylvestris* had no significant effect on litter mass loss. Some values are lower than zero as final litter weight was higher than initial weight in 24 cases (see main text for explanation). All the lines in the figure above are based on linear regressions (LM) with 95% confidence intervals.

Table 6
General linear model results of effects of earthworm presence, isopod presence, litter traits, and interactions on species-specific litter mass loss. These results are based on the best-fit model (based on AICc values) reduced from a full model including all interactions.

Factors	Residual dfs	Full model AICc	Best model AICc	F	p
Phenolic concentration	356	3388.2	3384.5		
Earthworm presence (E)				428.12	< **0.001**
Isopod presence (I)				30.43	< **0.001**
Phenolic concentration (P)				12.49	< **0.001**
E × I				11.04	< **0.001**
I × P				2.39	0.123
Tannin concentration	356	3387.4	3384.5		
E				429.03	< **0.001**
I				30.58	< **0.001**
Tannin concentration (T)				11.88	< **0.001**
E × I				10.87	**0.001**
I × T				2.98	0.085
Nitrogen content	357	3394.7	3390.4		
E				416.52	< **0.001**
I				29.15	< **0.001**
Nitrogen content				6.85	**0.009**
E × I				11.53	< **0.001**
Leaf thickness (without *Pinus*)	342	3252.0	3248.5		
E				421.04	< **0.001**
I				27.12	< **0.001**
Leaf thickness				8.61	**0.004**
E × I				12.36	< **0.001**
Leaf toughness (with *Pinus*)	356	3385.7	3382.5		
E				427.94	< **0.001**
I				30.12	< **0.001**
(L)				9.55	**0.002**
E × I				11.61	< **0.001**
E × L				7.38	**0.007**
Leaf toughness (without *Pinus*)	342	3244.8	3241.0		
E				420.42	< **0.001**
I				29.60	< **0.001**
L				9.39	**0.002**
E × I				11.39	< **0.001**
Surface leaf area	356	3395.0	3391.6		
E				417.39	< **0.001**
I				29.48	< **0.001**
Surface leaf area (S)				2.14	0.144
E × I				11.26	< **0.001**
E × S				5.55	**0.019**

Significant effects (p < 0.05) are highlighted in bold.

functional diversity on litter mass loss, based on repeated litter cover measurements (Fig. 2a). The strongest effect was an increase in litter mass loss in the presence of both macro-detritivore groups, supporting the notion that litter diversity effects are most pronounced with different detritivore species (Heemsbergen et al., 2004). The availability of more diverse resources might have led to resource partitioning and higher consumption efficiency among the detritivores. With a higher functional diversity, litter species differ more from each other in their traits, increasing the range of available food sources for macro-detritivores, and simultaneously the chances for finding the preferred litter species. In addition, the functional diversity of food sources in itself increases litter mass loss, even when less palatable litter species are present. This could be caused by chemical exchanges between litter species (Gartner and Cardon, 2004) or nutritional complementarity (Dudgeon et al., 1990; Vos et al., 2013). It is however not clear why litter mass loss was negatively (although weakly) affected by functional diversity in treatments with only one macro-detritivore group.

The effect of functional diversity on litter mass loss also changed over time during the experiment. The positive effect of functional diversity on litter mass loss increased over time in treatments including earthworms, suggesting that detritivore interaction effects on ecosystem functions are context-dependent. Towards the end of the experiment, the effect of functional diversity disappeared (Fig. A1), which may indicate that the decrease of available litter material led to a higher competition between the two macro-detritivore groups. In other studies, positive effects of the functional diversity of litter traits on decomposition have also been found in grasslands (Scherer-Lorenzen, 2008) and streams (Lecerf et al., 2011), despite the use of indices that differ greatly among studies. Neutral and negative effects of functional diversity have also been found in a mixed conifer forest litter decomposition experiment (Chapman and Koch, 2007) as we did for the isopod and earthworm treatments. The authors of that study found instead that the strongest synergistic effects of biodiversity on litter mass loss were with more closely related litter species, and suggest that the common well adapted bacterial community could process similar litter species more efficiently.

None of the litter trait community means influenced litter mass loss in mixtures. Instead, the MAD of C:N increased litter mass loss in all treatments, indicating that access to a more nutritionally varied diet increased the feeding activity of macro-detritivores. Vos et al. (2013) and Barantal et al. (2014) found similar results in that N dissimilarity increased litter mass loss in litter mixtures. Although we did not find that N dissimilarity influenced litter mass loss in our experiment (p > 0.05), both measures were related and confirm N content as an important litter trait.

While litter and macro-detritivore species differed greatly in identity effects on litter mass loss (Fig. 4; Gessner et al., 2010), it is
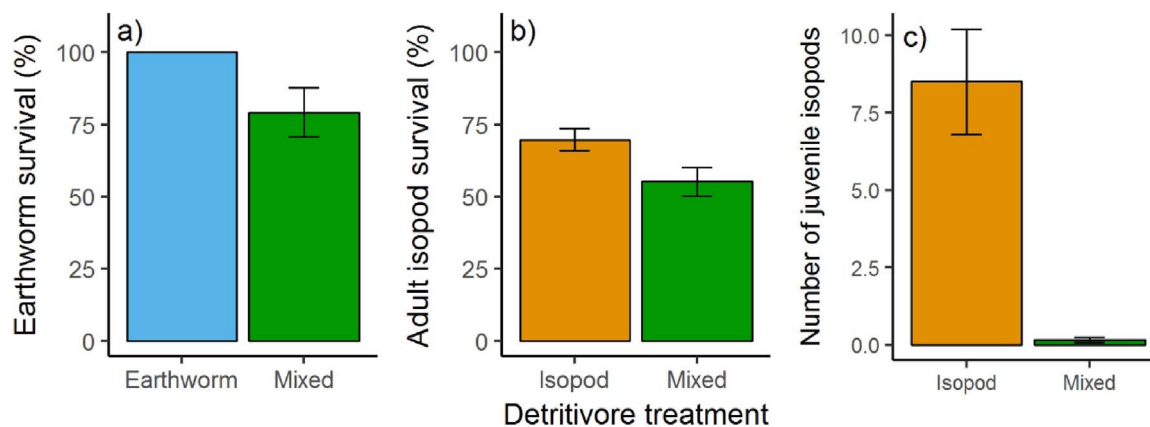

Fig. 6. a) Isopod presence influence on earthworm survival across litter treatments ($F_{1,46}$ = 14.4, p < 0.001). Earthworm presence influence on b) isopod survival ($F_{1,41}$ = 5.4, p = 0.025) and c) the number of juvenile isopods (reproduction) across litter treatments ($F_{1,41}$ = 42.8, p < 0.001). Means with standard error.

questionable if the consideration of the effects of detritivore species richness without specifically accounting for their traits would help to elucidate the mechanisms responsible for the inconsistent results in decomposition experiments using litter mixtures (Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Notably, detritivore functional diversity has been shown to be a more powerful predictor of litter mass loss and decomposition processes than detritivore species richness (Eisenhauer et al., 2010; Heemsbergen et al., 2004). Whereas detritivore species richness effects are thought to become saturated after the presence of two detritivore species (Heemsbergen et al., 2004; Zimmer et al., 2005), accounting for trait identity and dissimilarity effects of detritivores can be a promising approach to provide novel mechanistic insights and to derive general principles in the study of soil biodiversity effects (Bardgett and van der Putten, 2014; Powell et al., 2014).

4.3. Species-specific litter mass loss

We have not tested species-specific litter effects in pure litter, but always in mixed litters with three other species. These co-occurring species were always different for the 16 species studied (Table 1). Thus, the effects we reported here are mean identity effects from different mixtures. Because litter mass loss of single species depends on identity (i.e. functional traits) of co-occurring litter species (Hättenschwiler and Gasser, 2005; Scherer-Lorenzen et al., 2007a), the effects reported here should be interpreted cautiously. However, species-specific litter mass loss was influenced by numerous litter traits, as per our prediction.

Litter mass loss differed greatly among the 16 tested tree species (Fig. 4), with strong trait effects. The concentration of tannins and phenolics in the leaves is known to act as a defence against herbivores, which makes them crucial traits for litter decomposability (Coq et al., 2010; Freschet et al., 2012; Hättenschwiler et al., 2005; Wardle et al., 2002). Accordingly and in line with our expectations, the concentration of these compounds in the litter decreased litter mass loss in the present experiment (Fig. 5a and b; Table 6). In contrast to tannins and phenolics, leaf N concentration had a positive effect on litter mass loss (Fig. 5c; Table 6), as found in Cornwell et al. (2008). This is likely because the consumption of N-rich plant material is necessary for detritivores (Eisenhauer et al., 2009; Schwarz et al., 2015), in order to counter the nutrient imbalance between their bodies and food sources (Martinson et al., 2008). Surprisingly, the litter C:N ratio had no significant effect on litter mass loss, as C:N has been argued to be a better proxy of leaf quality than C and N concentrations alone (Hättenschwiler and Gasser, 2005). Leaf toughness decreased litter mass loss (Fig. 5e and f; Table 6) as the harder leaves might have been more difficult to break apart and consume (Gallardo and Merino, 1993). Leaf thickness, however, was surprisingly positively affecting litter mass loss (Fig. 5d, Table 6), for unknown reasons. Potentially, other unmeasured litter traits may have co-varied with leaf thickness.

While less palatable species were barely consumed, *F. excelsior*, *P. tremula* and *B. pendula* were some of the fastest decomposed litter species. This can be explained by their low content of secondary compounds (phenolics and tannins) and high nitrogen content (Hantsch et al., 2014). In addition, *F. excelsior* is known to decompose rapidly and has been found to contribute to litter mass loss in mixtures (possibly through a high P content; Vos et al., 2013). Isopods and earthworms had overall similar litter preferences (Fig. 4). It could be observed though that coniferous species (*L. decidua* and *P. sylvestris*) were consumed less by earthworms, but were among the preferred species of isopods, indicating a potential for resource partitioning between the two macro-detritivores. Coniferous litter (Hobbie et al., 2006), and specifically *L. decidua* (Schwarz et al., 2015), have been found to reduce earthworm density under field conditions, which indicates an avoidance of these species. The acidity of the litter, as well as the presence of terpenoids may explain the low palatability for earthworms (Croteau et al., 2000; Edwards, 2004).

The litter mass loss of the very recalcitrant species *Q. petraea*

showed no change with detritivore presence, and *Fagus sylvatica* only a very weak effect. The high tannin content (and lignin content) of the leaves is often used to explain the low feeding intensity on *Quercus* species and *F. sylvatica* (Edwards and Heath, 1975; Hättenschwiler and Gasser, 2005). This could, however, not be confirmed in the present study, as *Q. petraea* and *F. sylvatica* did not have exceptionally high tannin contents (nor phenolic content, C:N, leaf toughness, or leaf thickness) compared to other species in the pool (Hantsch et al., 2014). *Quercus* species and *F. sylvatica* litters are often found to have very slow breakdown rates (Hättenschwiler and Gasser, 2005; Vos et al., 2013, 2011). However, litter mass loss of *Q. petraea* was found to only be influenced by litter diversity in the presence of millipedes (Hättenschwiler and Gasser, 2005), with no effect of diversity in the presence of isopods or earthworms. These results suggest a potential specialization of macro-detritivores in the degradation of more persistent litters. While high quality litter is preferred by many macro-detritivores, overall less attractive litters might still be palatable for certain groups of macro-detritivores that are well adapted to process specific secondary compounds or tougher materials. Further research will be needed to explore these hypotheses.

4.4. Fauna performance

While we found some degree of resource partitioning among the macro-detritivore groups, strong competition dynamics were also observed. The performance of both macro-detritivore groups was reduced in the mixed treatment compared to treatments with only one macro-detritivore group, indicating competition for surface litter material as a food source (and habitat for isopods). It is not clear if these effects on population dynamics of the two macro-detritivore groups are the result of direct or indirect interactions among the two groups, and this topic needs further investigation. The survival rate of earthworms was decreased in the presence of isopods (Fig. 6a). However, surprisingly, elevated mortality levels of earthworms were not reflected by a negative weight change in the microcosms of the mixed treatment where earthworms survived. The negative effect of isopods on earthworm survival remains unclear. We speculate that increased earthworm mortality might have been caused by direct aggressive interactions with isopods, but might also be due to an increased pathogen load when isopods are present. In turn, the presence of earthworms also reduced the survival rate of isopods (Fig. 6b). The ways in which earthworms might negatively impact other soil invertebrates like isopods are manifold (Eisenhauer, 2010). First, anecic earthworms (as used in this study) mix the litter layer and remove litter material from the soil surface by pulling it into its burrows, before consuming it there (Edwards, 2004). In addition to competition for resources, this activity may negatively affect isopods by reducing the availability of favoured litter material and disturbing as well as by removing their habitat (Eisenhauer, 2010). Furthermore, earthworms have substantial effects on soil structure through the formation of vertical burrows. Surface water thus infiltrates more quickly in the ground through earthworm burrows functioning as preferential flow pathways, and the soil surface dries faster (Edwards, 2004; Fischer et al., 2014). Drier soil surface has been shown to detrimentally affect isopod performance, as these animals require moisture (Paris, 1963; Wright and Machin, 1990). Soil water content measurements at the end of the present experiment, however, did not show significant changes in soil moisture between earthworm treatments, but the expected changes due to earthworm presence might have been at a smaller scale or variant in time. The negative effect of earthworm presence on isopod performance was also visible in data on isopod reproduction, where earthworm presence strongly decreased the number of juvenile isopods (Fig. 6c). This might have been caused by a reduced fertility of adult isopods due to higher stress and inadequate feeding in the mixed treatment, or by the direct destruction of juveniles by earthworms.

In another experiment where five isopods and one earthworm were

used together in microcosms to test their effect on tree litter mass loss for a similar period as in our experiment, Zimmer et al. (2005) found a mortality rate of 2% for earthworms and isopods, with no significant effect of the presence of the other macro-detritivore. While the difference with our findings (10% mortality for earthworms, 29% mortality for isopods, Fig. 6a and b) is striking, this might be in part due to the earthworm species used. In Zimmer et al. (2005), the earthworm species *Lumbricus rubellus* that was used is an epi-endogeic earthworm, which does not show the same litter burrowing behaviour of *L. terrestris* (Edwards, 2004). This significant difference might have reduced the negative interaction between macro-detritivores in Zimmer et al. (2005), as the litter material was not removed in burrows, and earthworm effects on water infiltration might have been less pronounced.

The negative effects of earthworm presence on isopod population dynamics may have particularly strong consequences in multi-generation experiments or in natural systems by limiting isopod population growth. In forest habitats, a plethora of other detritivore groups are also present, such as millipedes (Diplopoda) and mites (Acari). Future studies should investigate detritivore species interactions of more complex communities and explore if competition is further increased with the presence of more diverse detritivore fauna or if trophic interactions with predators are necessary to regulate detritivore communities, especially as competitive interactions among litter-dwelling detritivores are likely to increase with time after litter fall and resources become scarce.

5. Conclusions

In conclusion, we found support for hypothesis (1b) as the strong competition between the macro-detritivores led to less than additive effects on litter mass loss when both groups were present. The effects of functional diversity on litter mass loss depended on the macro-detritivore community and time in the present study, with the strongest effect in the presence of both macro-detritivore groups, supporting hypothesis (2). Our highly-resolved temporal data on litter mass loss revealed that, overall, the effect of the mixed macro-detritivore treatment on litter mass loss was highest at high functional diversity of litter traits, supporting the notion that litter diversity effects are most pronounced in the presence of different detritivore species (Gessner et al., 2010). While mean trait values were not found to influence litter mass loss in mixtures as hypothesized in (3), dissimilarity in C:N ratios increased litter mass loss, potentially by providing a more balanced diet and nutrient sources for macro-detritivores. Species-specific litter mass loss was explained by nutrient content, secondary compound concentration and structural components, revealing similar results as previously found in decomposition experiments with monocultures. Based on preferences observed from this and other studies (Hättenschwiler and Gasser, 2005), we expect that more numerous detritivore groups might not increase species-specific litter mass loss for high-quality litter mixtures, but that litter mass loss of lower-quality litters would be increased with the presence of complementary detritivore species well adapted to reduce those specific litters.

The strong competition for soil surface litter between the two macro-detritivore groups in this experiment and the related increase in mortality rate for both groups when present together may be informative of strong local competitive interactions in natural conditions with progressive litter decay. Based on this study, the loss of tree biodiversity, and especially functional diversity, might contribute to a decrease in ecosystem functions, especially decomposition and nutrient cycling. Thus, the temporal dynamics of litter trait diversity effects and their interaction with detritivore diversity are key to advancing our understanding of litter mass loss in nature.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pedobi.2017.07.003.

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