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Do invertebrate decomposers affect the disappearance rate of litter mixtures?

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Abstract

We designed an experiment using litter bags with fine and coarse mesh size to analyse interacting effects between invertebrate decomposers and the number of litter species on litter disappearance rates. We used litter of nine broad-leaved tree species to compare disappearance rates of litter from single species with mixtures of two to six species. Species composition of litter and invertebrates interacted strongly in their effects on litter disappearance rate. Contribution of invertebrates to litter disappearance increased with time mainly for litter which disappeared slower in the absence of invertebrates. Disappearance rates were positively correlated with initial N content and negatively correlated to initial C content of litter. These relationships were stronger in the presence of invertebrates, suggesting that their activity is positively related to initial litter chemistry. Number of component litter species, however, had no effect on disappearance rate irrespective of the activity of invertebrates. Using individual rates of disappearance for single species, we calculated the expected rates of disappearance for each of the experimental mixtures of leaf litters. We found that mixtures of several species of leaf litter resulted in significant deviations from the expected values. These deviations showed a significant effect of the number of component litter species. However, this result was caused by a strong negative deviation of one single mixture of six species. The presence of invertebrates resulted in even greater deviations from the expected values, suggesting an important contribution of invertebrates to the effects of litter mixing on litter disappearance rates. Hence, our results underline the importance of idiosyncratic effects of species traits in mixtures. Our results suggest that the influence of invertebrate decomposers interacts with litter chemistry during decomposition, but is not affected by litter species richness per se.

Keywords: Biodiversity; Broad-leaved trees; Decomposer fauna; Litter C and N contents; Litter decomposition; Litter mixtures

1. Introduction

The importance of biological diversity as a regulator of ecosystem processes and dynamics is a hotly debated issue in ecology (Loreau et al., 2002). After a decade of a above-ground centred view on this topic, the importance of soil processes and 'after life effects' (Findlay et al., 1996) of plant diversity is increasingly recognised (Wardle, 2002). Numerous investigators have explored the effect of litter diversity on decomposition rate. In a review of decomposition rates in mixtures (litter from two or more plant species) with expectations from experiments with single litter types, Wardle (2002) found that neutral, positive and negative effects are possible. However, any effect on decomposition rate should be attributed to a changed activity of the decomposer community in these mixtures. Litter decomposition results from the activities of soil microbiota and invertebrates. The relative importance of invertebrates differs from site to site (Swift et al., 1979; Seastedt, 1984; Heneghan et al., 1998), but may also differ between litter types and specific litter mixtures. Further, different species of invertebrates may be attracted to certain litter types. Therefore, with an increasing richness of litter species decomposers may show complementary resource use and, thereby, increase decomposition rates in litter mixtures. Thus, the activity of invertebrates may influence the relationship between litter diversity and decomposition rates.

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Table 1
Results of nested ANOVA on the effect of litter species richness, mixture, time and invertebrate fauna on decomposition rate of litter samples and deviation of remaining litter mass in mixtures from expected values

Source	Disappearance rate				Deviation from expected values			
	df	MS	*F*	*P*	df	MS	*F*	*P*
[*F*] Fauna	1	10.71	2940.14	<0.001	1	891.93	3.23	0.07
[*S*] Species richness^{A}	3	0.03	0.06	n.s.	2	2023.35	5.76	0.02
[*M*] Mixture$(S)^{a}$	20	0.53	145.46	<0.001	12	351.09	1.27	n.s.
[*T*] time	1	5.35	1469.29	<0.001	1	2245.53	8.14	0.005
$F\times S^{B}$	3	0.01	0.05	n.s.	2	1068.47	7.52	0.007
$F\times M(S)^{b}$	20	0.10	26.80	<0.001	12	142.07	0.51	n.s.
$F\times T$	1	0.26	71.10	<0.001	1	774.83	2.81	0.10
$S\times T^{C}$	3	0.01	0.22	n.s.	2	138.38	0.21	n.s.
$M(S)\times T^{c}$	20	0.02	5.88	<0.001	12	648.73	2.35	0.007
$F\times S\times T^{D}$	3	0.01	0.17	n.s.	2	16.43	0.03	n.s.
$F\times M(S)\times T^{d}$	20	0.02	4.66	<0.001	12	488.33	1.77	0.05
Block	4	0.02	6.32	<0.001	4	230.05	0.83	n.s.
Residual	380	0.01			236	276.45		

Terms indicated by upper case letters were tested against the term with the same lower case letter; all other terms were tested against the residual.

The diversity of litter may mould the diversity and activity of decomposers. However, Wardle (2002), Wardle and van der Putten (2002) and Gartner and Cardon (2004) found no consistent effect of litter diversity on diversity and abundance of invertebrates. Further, an increased invertebrate diversity may not necessarily translate into higher decomposition rates. Some authors argue that the diversity of decomposers may have only minor effects on ecosystem functions due to complex trophic interactions and high functional redundancy in decomposer food webs (Mikola et al., 2002; Wardle, 2002). Thus, it is difficult to predict the effects of invertebrate decomposers on litter decomposition rate from the diversity of soil invertebrates. The assessment of decomposer diversity in litter mixtures may not be a suitable predictor for interacting effects of invertebrate activity and litter species richness. Experimental manipulation of decomposer invertebrates is necessary to examine these processes. We could not find published studies that have investigated the interaction between the activity of soil invertebrates and litter diversity on decomposition rates.

In our study we aim to answer the following questions: (1) Is there an effect of the invertebrate decomposer fauna on litter disappearance rates of litter types and multiple species mixtures? (2) Do the effects of the number of component litter species and the activity of invertebrate decomposers interact in their effects on litter disappearance rates? and (3) Can these effects be related to initial C and N contents of litter as a measure of litter quality?

2. Material and methods

2.1. Experimental setup

Freshly fallen leaf litter of nine broad-leaved tree species (Appendix) was sampled in autumn 2001. We collected litter without visible signs of decomposition, herbivory or pathogens. Litter was cleaned by brushing, then dried and stored at room temperature. A subsample of litter from each tree species was ground in a mill. Total N and C contents of these samples were measured with an Elementar Vario EL element analyser (Elementar Analysengeräte GmbH, Hanau, Germany).

Litter bags with 1 l type were established using 3 ± 0.2 g of air dry litter of each tree species. In addition to all possible monocultures, three diversity levels (referring to the number of component litter species) were created by random draws from the species pool (Appendix).

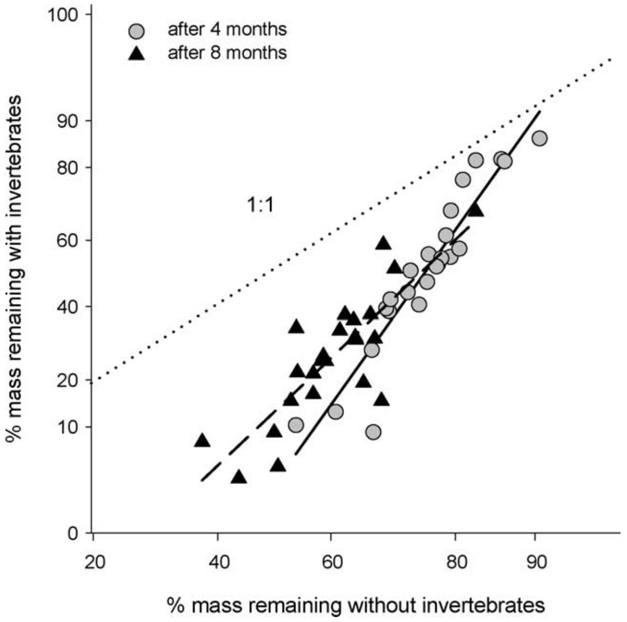

Fig. 1. Relationship between litter mass remaining in the bags without and with invertebrate decomposers after 4 months (circles and solid line, $R^2=0.89$, $P<0.001$) and after 8 months (triangles and dashed line, $R^2=0.69$, $P=0.048$). Every symbol refers to the mean of a specific litter type or litter mixture across all blocks (five replicates). The 1:1 line is shown by the dotted line. Note that the axes are arcsin-square root transformed.

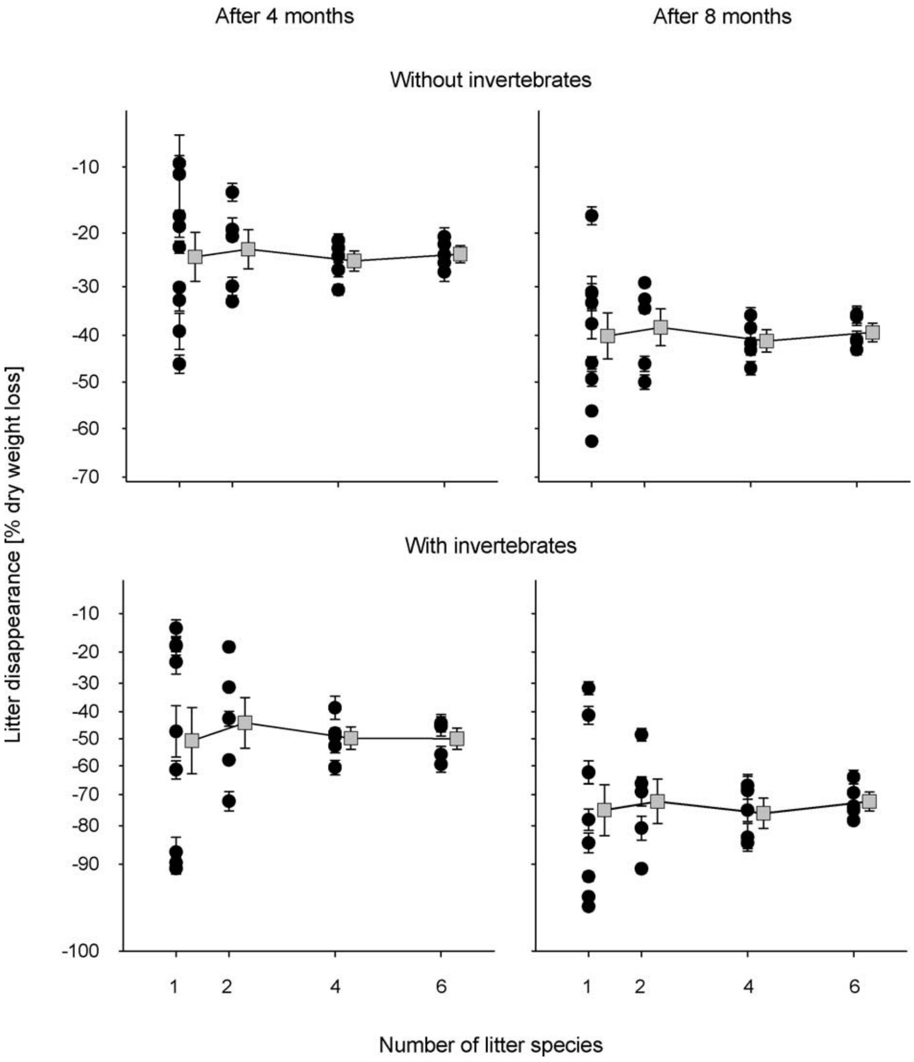

Fig. 2. Disappearance rate (percentage dry weight loss) of litter samples for all litter species and mixtures (black points; mean ± standard error, five replicates per mean) and diversity levels (grey squares, mean ± standard error with species and mixtures as replicates, nine replicates for monocultures and five replicates for mixtures) for the two sampling dates without (a, b) and with invertebrate fauna (c, d). Note different scaling of *y*-axes of top and bottom panels.

We set up five two-species mixtures with 1.5 ± 0.1 g per species, five four-species mixtures with 0.75 ± 0.05 g per species and five six-species mixtures with 0.5 ± 0.03 g per species. Our experimental design replicates both number of component species and composition and, thus, permits separation of the effects of species composition and of diversity (Schmid et al., 2002). Dry weight of every species was multiplied with the corresponding N and C contents to calculate initial element contents. Each litter mixture and monoculture was replicated 20 times. To fill the litter bags, we moistened the litter with deionised water to avoid breakage. Half of the replicates were placed in nylon bags with a mesh size of 5 × 5 mm^2. This mesh size allows the passage of soil invertebrates. For the remaining replicates we used bags with a mesh size of 20 × 20 $\mu\mathrm{m}^2$ to exclude soil invertebrates. This mesh is fine enough to allow access by bacteria, fungal hyphae, most nematodes, and protozoa, while restricting access by mesofauna and macrofauna. In April 2002, litter bags were randomly placed in five plots (two replicates within each plot) on bare ground of a mixed forest stand dominated by *Betula pendula*, *Quercus robur* and *Fagus sylvatica* near Marburg (Hesse, Germany, 50° 48′0N, 8°48′0E, 325 m NN). Plots were 2 × 2 m^2 and randomly distributed across an area of about 15 × 20 m^2. Plots were covered with a net (mesh size 5 × 5 mm^2) to prevent natural litter fall from disturbing our experiment.

Half of the samples (one replicate from each block) were removed from the field after 4 months and the remaining bags after 8 months. Remaining litter was dried, cleaned and weighed. Percentage dry weight loss was defined as disappearance rate.

2.2. Data analysis

Prior to statistical analysis disappearance rates and percent N and C data were arcsine square-root-transformed

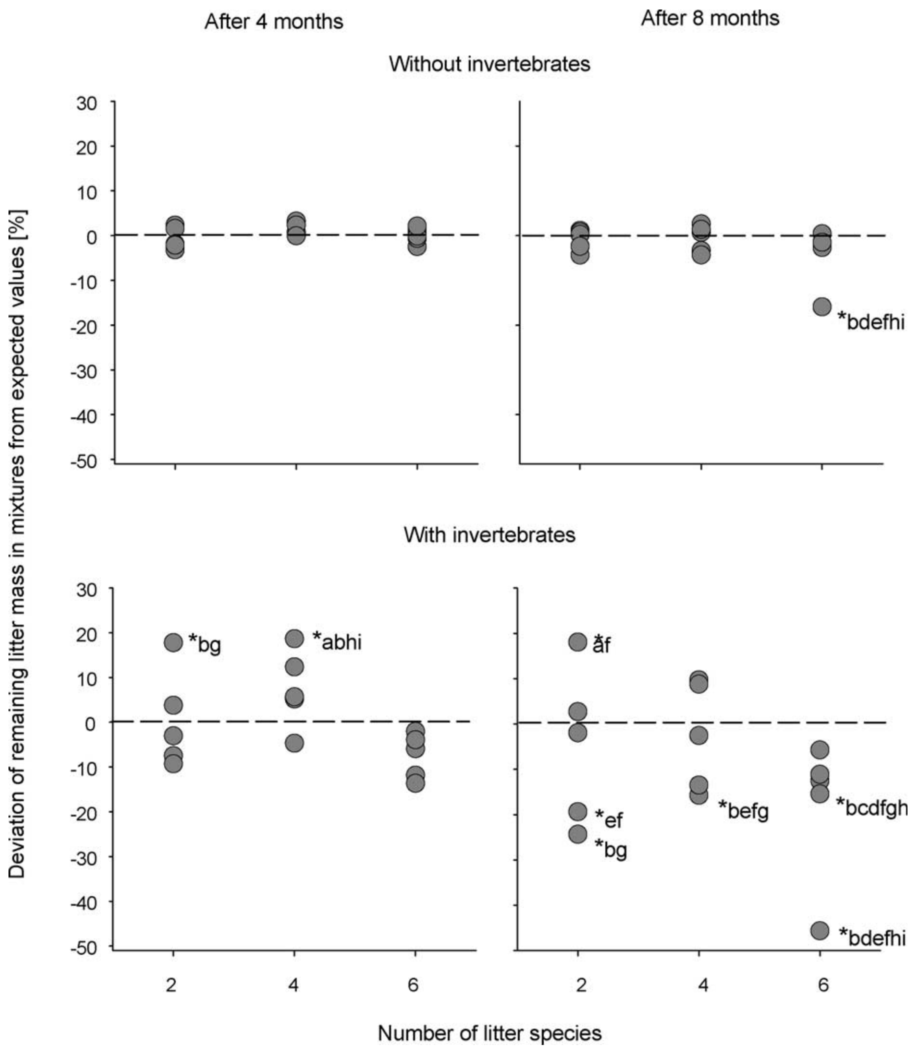

Fig. 3. Percentage deviation of remaining litter mass (dry weight) in mixtures from values which would be expected from disappearance rates of monocultures without (a, b) and with invertebrates (c, d). Each symbol refers to the mean of a specific mixture across all blocks (five replicates). Asterisks indicate significant deviation from zero (no overlap with 95% confidence interval) after Bonferroni correction. Overlap of data (see Appendix) results in less than five visible symbols per diversity level in some cases.

to reduce heterogeneity of variances (Bartlett's test) and non-normality (Kolmorgorov–Smirnov test). We used a nested general linear model (Proc GLM in SAS 8.2) to test for effects of fauna, time, diversity and species composition (nested in diversity) on disappearance rates. Plots were considered as blocking factor in the analyses. Disappearance rates of monocultures were used to calculate expected dry weight of litter remaining in litter mixtures, which assumes that there are no diversity effects (i.e. mixture rates are additive sums of monoculture rates):

$$R_e = \sum_{i=1}^{S} m_i p_{m_i}$$

where m_i = initial mass of litter of species i in mixture and p_{m_i} = disappearance rate of species i without other species. This equation is similar to the formula used by Blair et al. (1990) and Wardle et al. (1997), but takes into account differences in initial litter masses of component species. Observed litter masses remaining in mixtures (R_o) in relation to expected values were calculated as $[100\times(R_o-R_e)/R_e]$ per block (see Wardle et al. (1997)). Deviations from zero were tested using 95% confidence intervals. Effects of fauna, time, diversity and species assemblage (nested in diversity) were again tested using a nested general linear model (Proc GLM in SAS 8.2). The influence of N and C contents on disappearance rate were tested using linear regression and ANCOVA.

3. Results

3.1. *Effects of excluding invertebrates*

The exclusion of invertebrates markedly decreased litter disappearance rates (Table 1, Appendix, Fig. 1).

However, this effect differed considerably between litter bags containing different species compositions. Percentage litter mass remaining in the presence of invertebrates was positively related to remaining litter mass without invertebrates, indicating a close relationship of litter palatability to invertebrates and microbiota. This relationship was stronger after 4 ($r=0.95$) than 8 months ($r=0.83$; comparison of correlation coefficients, $P<0.01$). Both slopes (2.4 after 4 months, 1.6 after 8 months) were significantly higher than 1 (95% confidence intervals) with the fastest disappearing litter types and mixtures showing the greatest deviation from the 1:1-line which would indicate no effect of invertebrates. Further, the regression line of this relationship was significantly less inclined after 8 months due to a greater relative contribution of invertebrates to mass loss of slow disappearing litter (ANCOVA, $P<0.01$, Fig. 1).

3.2. *Effects of mixing litter species*

The specific species composition of litter had a striking influence on disappearance rates, yet number of component litter species per se did not (Table 1, Appendix, Fig. 2). Further, there was a decreasing variability of disappearance rates with increasing number of component litter species due to the increasing similarity in the composition of mixtures. The effect of invertebrates on disappearance rates was contingent on the specific mixture (highly significant interaction) but did not interact with the number of component litter species (Table 1, Fig. 2). Time did not only affect disappearance rate in general, but also interacted with the activity of invertebrates (see above) and species composition of litter (Table 1), indicating different decomposition dynamics of different litter mixtures.

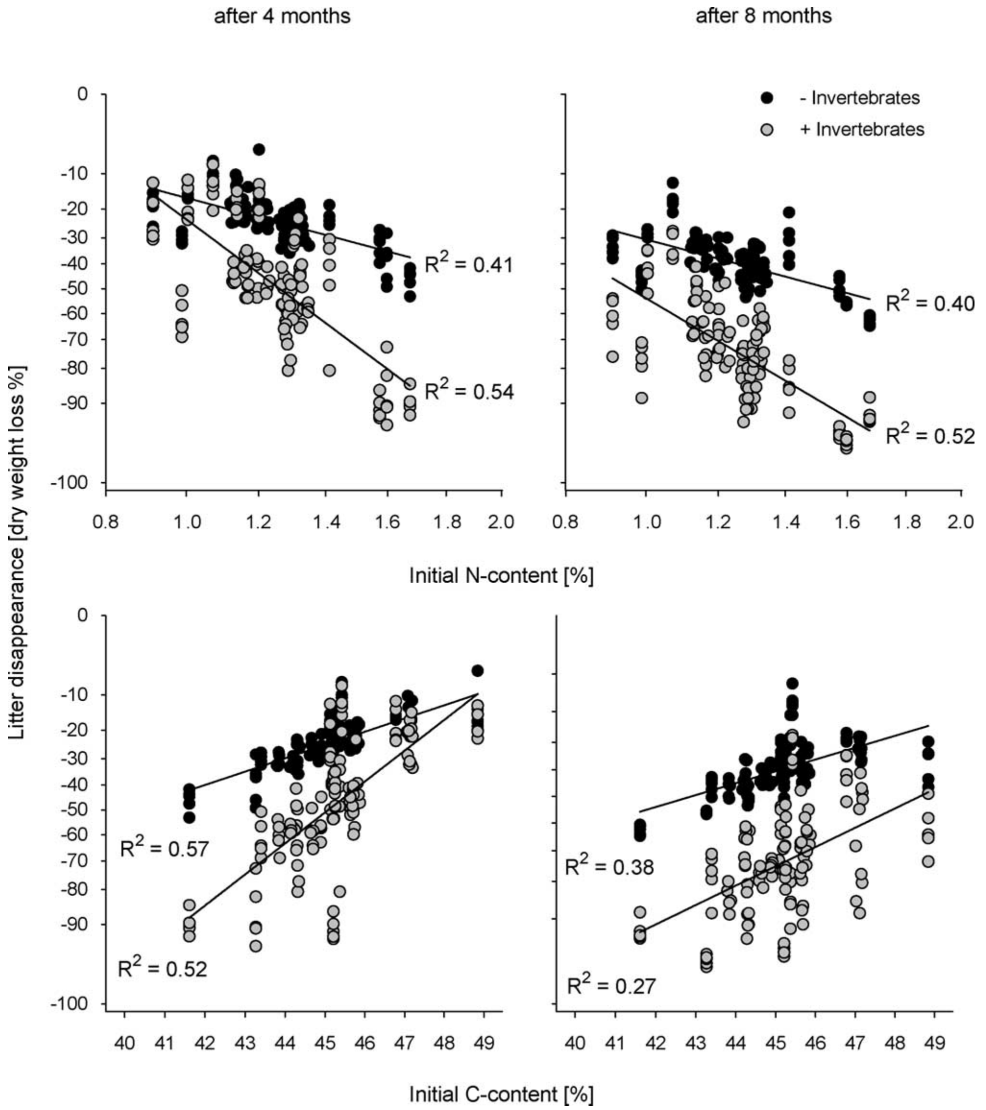

Fig. 4. Relationship between disappearance rate of litter samples and initial contents of nitrogen and carbon at the two sampling dates with (grey circles) and without invertebrate fauna (black circles; $P<0.001$ all correlations). Symbols represent all litterbags used in the study.

3.3. Deviations from expected values

For litters exposed to invertebrates, litter mass remaining in bags with mixtures showed strong deviations from the values expected from the disappearance rates in bags containing one litter type. However, few values were significantly different from zero (Fig. 3). Across all mixtures and sampling dates, the invertebrates had a slight effect on the percentage deviation (−4.3%, Table 1). However, we found a significant interaction of the effect of invertebrates with litter species richness (Table 1). When averaged within a diversity level, only in mixtures with six species invertebrates generated a strong deviation from the expected values (mean with invertebrates: −12.8%, mean without invertebrates: −2.1%). In the four-species mixtures (mean with invertebrates: 2.4%, mean without invertebrates: 0.4%) and two-species mixtures (mean with invertebrates: −2.3%, mean without invertebrates: −0.7%) invertebrates had only a slight influence. However, the effect of species richness was generated by a large negative deviation from the expected value in a single litter mixture (*Fraxinus excelsior*+*Quercus rubra*+*Acer platanoides*+*Corylus avellana*+*F. sylvatica*+*Tilia tomentosa*) in both treatments with or without invertebrates (Fig. 3). Again, beside the general effect on deviations from expected values, time interacted significantly with the species composition of litter mixtures (Table 1). For example the mixture consisting of *A. platanoides* and *Cerasus avium* showed a significant positive deviation in the presence of invertebrates after 4 months and a significant negative deviation after 8 months (Fig. 3, indicated by the index bg, see Appendix).

3.4. Effects of litter C and N contents

C and N content were not correlated across litter types ($P>0.1$) and showed independent effects on disappearance rates of litter (multiple regression, effects of both variables significant with $P<0.05$). Disappearance rates were negatively correlated to initial C content. This relationship was strongest after 4 months (comparison of correlation coefficients, $P<0.05$). Furthermore, the negative slope of this relationship was steeper for litters exposed to invertebrates (ANCOVA, $P<0.001$) due to higher disappearance rates in samples with low initial C content. Disappearance rate was positively correlated to N content in litter. Again, the slope of this relationship between disappearance rate and initial N content was steeper for litters exposed to invertebrates (ANCOVA, $P<0.001$) due to higher disappearance rates with invertebrates in litter samples with high initial N contents (Fig. 4).

4. Discussion

4.1. Effects of excluding invertebrates and litter chemistry

The use of litter bags with different mesh sizes is a common approach for the assessment of the contribution of soil fauna to litter disappearance. Differences in mass loss between coarse and fine mesh of litter bags are usually attributed to the activity of invertebrates. We are aware that increasing mesh size will also increase the loss of material as a result of fragmentation of litter. However, following Anderson (1973) fragmentation of leaves is a part of the catabolic degradation of litter. We therefore agree with Bradford et al. (2002) and consider the breakdown and loss of small litter fragments from the sample as a functional role of decomposer fauna.

Although the effects of invertebrates on disappearance rate was generally large in our study, this effect differed considerably between litter types and mixtures. Remaining litter mass with and without invertebrates were correlated indicating that there are generally slow and generally fast decomposing litter types and mixtures. For slow disappearing litter, however, contribution of invertebrates decomposers to litter disappearance was lower than for the fast disappearing litter. This effect was weaker after 8 months. This indicates a rapid initial breakdown of high-quality litter, whilst for low-quality litter the effects of invertebrates increased with time. This may be explained with changes of litter chemistry during the decomposition process, what may influence the activity of decomposers (Berg et al., 1982). These changes often result in a loss of C-based secondary compounds (e.g. phenolics, see Schofield et al. (1998)) and an increased degradability of leaves. Moreover, Hunter et al. (2003) showed that the activity of macroinvertebrates (mainly predators) contributed to changes in the chemistry of litter during decomposition, presumably through their effects on microinvertebrates and the microbiota. Numerous investigators have shown that litter decomposition is influenced by initial C and N concentrations (Swift et al., 1979; Shädler et al., 2003; but see Schaefer et al., 1985; Wardle et al., 2003). In our study, disappearance rate was negatively affected by the C and positively affected by the N content of the litter. These effects were stronger with, than without, invertebrates. The positive effects of invertebrates on disappearance rates was highest in N rich and C poor litter. However, Smith and Bradford (2003b) found that litter quality (defined as initial N content) effects on decomposition was differently related to complexity of soil fauna across two sampling dates. Maity and Joy (1999) and Zimmer and Topp (2000) demonstrated that the abundance and activity of invertebrates is often influenced by the initial chemistry of litter. Since contribution of fauna to disappearance increased with time only for the slow decomposing litter, our results suggest that the suitability of low-quality litter as a food source for invertebrates increases during decomposition. Berg and Matzner (1997) and Berg (2000) suggest that interactions based on different N and lignin content of litter might be more pronounced in the last phase of the decomposition process. However, the duration of 8 months used in our experiment may not cover this phase of decomposition for some of the used slow decomposing litter species (e.g. oak, beech, plane). Therefore, in the longer run the observed effects may slightly differ.

4.2. Effects of mixing litter species

Although we found considerable effects of soil invertebrates and the composition of litter on disappearance rates, number of component litter species per se showed no effect during our study. In keeping with the 'variance reduction effect' (Huston, 1997), variability of decomposition rates decreased with increasing litter diversity in our study due to an increasing similarity of composition in the mixtures. According to Fukami et al. (2001), this may be considered as one of the mechanisms behind the increase of ecosystem reliability (the probability that a system will provide a consistent level of performance) with increasing biodiversity.

In a study using herbaceous litter, Hector et al. (2000) found a trend of increased decomposition rates with diversity of mixtures. Other studies failed to show any consistent pattern (Chapman et al., 1988; Blair et al., 1990; Wardle et al., 1997). In our experiment, we further found no evidence for interacting effects of the activity of invertebrates and litter species richness on disappearance rate. Despite the fact that we used a quite diverse forest stand (eight tree species across the experimental site, but only in part the same as those used in our study) for our experiment, there is always the possibility that the local decomposer community is adapted to the specific site conditions and litter composition. Therefore, we examined the effects of number of component litter species on disappearance rate contingent on the decomposer community present at our site. Further, some of the used litter mixtures do occur in nature, whereas other mixtures consist of litter from species that do not occur together in native ecosystems. It may be assumed that decomposing organisms have co-evolved with the litter of certain species or certain litter mixtures for that matter. However, disappearance rates for alien species (*Q. rubra, Platanus* × *hispanica, T. tomentosa*) did not differ from native species neither with (mean ± standard error for aliens: 67.0 ± 16.3, natives: 74.1 ± 9.8) nor without invertebrates (mean ± standard error for aliens: 41.7 ± 7.5, natives: 40.0 ± 6.5). Furthermore, our experiment did not assess long-term effects of litter diversity on the composition of the invertebrate community (see also the results of Zimmer (2002)).

4.3. Deviations from expected values

Although the number of species in mixtures had no influence on disappearance rates in our experiments, it was obvious that total disappearance rates of mixtures may differ from expected values predicted from individual experiments with each litter type containing in the mixtures. Hence, our results suggest that invertebrates contribute to this effect importantly. When averaged across all mixtures, disappearance rates were significantly lower than expected only in experiments with access of invertebrates. However, in our experiment, this effect as well as the significant effect of litter diversity on the deviation from expected values was generated by a strong negative deviation in one single mixture of six species. We found this deviation in bags containing that mixture with as well as without access of invertebrates collected after 8 months across all plots. We are not able to explain this strong effect of one specific mixture, which shares three or four species with all other six-species mixtures used in our experiments. Nevertheless, our result serves as an example for strong idiosyncratic effects of species on ecosystem processes. Such unpredictable non-additive effects of litter mixing on decomposition rates were found by Chapman et al. (1988), Blair et al. (1990), Wardle et al. (1997) and Bardgett and Shine (1999). Our study suggests that the activity of invertebrates enhances these idiosyncratic effects. In a recent review on litter mixing experiments, Gartner and Cardon (2004) found a trend to an increased decomposition rate when litters of different species are mixed. From our results we conclude that these effects may be due to the activity of soil fauna.

Seastedt (1984) suggested that the decomposition rate of litter of a species may increase when this species has been mixed with high quality litter and decrease when mixed with low quality litter. In contrast, using litter bags with two compartments Wardle et al. (2003) showed for Swedish boreal forests that slow decomposing litter had the greatest positive effects on decomposition of associated litter. This may be due to the retention of moisture by slow decomposing litter and contrasts with results of Wardle et al. (2002) in a moist New Zealand rainforest. Hoorens et al. (2003) showed that differences between observed and expected decomposition rates in mixtures were not related to differences in litter chemistry of the component species. However, Smith and Bradford (2003a) found that mixing litter of the same species but with different N concentrations generally decreased decomposition rates, indicating confounding effects of correlated litter traits in experiments with litter from different species. Many factors more may have contributed to unexpected amounts of remaining litter mass in the samples. For example massive fungal hyphal development on the litter which may have physically prevented invertebrate colonisation, removal of litter fragments or litter palatability. However, there was no obvious sign of massive fungal growth in our bags. It may further be supposed that interactive effects among different litter types may further involve chemical interactions between litter secondary compounds.

4.4. Conclusions

Independent from the activity of invertebrates, number of component litter species had no significant effect on litter disappearance rates. The relative contribution of invertebrates to disappearance differed considerably between litter types and mixtures and was positively affected by higher litter quality (defined as high initial N and low initial C concentration). Artificial mixing of litter had idiosyncratic effects on disappearance rates. Further, the activity of invertebrates contributed importantly to the effects of litter mixing on relative deviations of remaining litter mass in mixtures from expected values across all levels of litter richness. Therefore, invertebrate decomposers interacted with specific composition of litter but not with litter richness per se to determine disappearance rates.

Appendix

Litter species with initial N and C concentrations and mixtures (listed in ascending order of N content). Letters for the mixtures correspond to species in the monocultures column. Litter disappearance rate (% dry weight loss) of litter species and litter mixtures used in the study and deviations of remaining litter mass in mixtures from expected values referring to mesh size and time (mean ± standard error). Values in bold represent significant deviations (see Fig. 3).

	N (%)	C (%)	Disappearance rate (%)				Deviation from expected values (%)			
			After 4 months		After 8 months		After 4 months		After 8 months	
			Coarse mesh	Fine mesh	Coarse mesh	Fine mesh	Coarse mesh	Fine mesh	Coarse mesh	Fine mesh
Monocultures										
(a) *Quercus robur*	0.91	45.1	23.6±2.7	19.0±1.5	62.0±3.0	33.3±1.2				
(b) *Acer platanoides*	0.99	43.4	61.2±2.4	30.2±0.6	77.8±2.3	45.9±1.0				
(c) *Platanus×hispanica*	1.00	46.8	18.6±1.9	17.2±0.7	41.4±2.4	31.1±1.2				
(d) *Fagus sylvatica*	1.07	45.4	13.8±1.6	9.6±0.7	31.8±1.7	17.2±1.1				
(e) *Quercus rubra*	1.20	48.8	18.2±1.4	14.4±1.9	62.2±3.1	37.7±2.3				
(f) *Corylus avellana*	1.41	45.4	47.0±6.7	22.6±0.8	84.4±1.9	31.6±2.5				
(g) *Cerasus avium*	1.57	45.2	90.8±0.9	32.8±2.8	96.0±0.2	49.4±1.2				
(h) *Tilia tomentosa*	1.60	43.2	86.3±2.9	39.3±1.1	97.3±0.2	56.3±0.2				
(i) *Fraxinus excelsior*	1.67	41.6	89.6±1.0	46.2±1.5	92.5±0.8	62.7±0.6				
2-Species mixtures										
af			42.6±2.7	19.6±1.9	68.7±4.6	32.5±0.7	−9.3±8.7	1.6±2.6	**18.0±15.0**	0.2±2.9
bg			72.0±3.2	33.0±0.9	90.9±1.0	50.5±1.5	**17.8±14.9**	−2.0±2.9	−**24.3±14.4**	−4.3±4.1
ci			57.8±0.6	30.3±1.7	66.2±2.3	46.1±1.0	−7.5±2.4	2.3±2.5	2.7±10.5	1.1±3.7
de			18.7±1.3	13.6±1.3	48.5±2.3	29.3±0.9	−3.1±1.9	−2.1±3.0	−2.0±4.8	−2.4±2.7
ef			31.4±0.8	20.6±0.5	80.2±3.5	34.4±1.0	3.8±9.1	−3.2±2.0	−**19.3±20.7**	0.8±3.1
4-Species mixtures										
abhi			60.5±2.6	30.7±1.0	84.7±1.5	47.1±1.4	**18.7±8.9**	2.3±2.1	−13.5±11.0	1.4±2.7
acfg			47.9±1.9	22.8±1.5	68.2±5.7	35.8±1.6	−4.6±6.1	0.1±2.2	9.7±19.0	0.7±6.2
bcfi			49.1±2.4	26.7±1.3	74.9±3.6	41.7±2.3	12.3±9.5	3.2±1.7	−2.6±12.7	2.6±5.7
befg			52.6±2.6	24.2±1.1	82.6±3.8	43.1±1.1	5.2±9.2	0.8±2.2	−**15.7±12.4**	−3.4±1.9
defh			38.8±4.0	21.4±1.2	66.7±3.1	38.5±2.0	5.7±7.8	− 0.1±1.8	8.8±13.2	−4.3±2.9
6-Species mixtures										
abcdfg			45.5±3.6	22.0±1.0	69.1±4.4	35.7±1.8	−3.9±7.1	−0.1±2.0	−11.1±10.4	−1.5±2.2
abcdge			45.0±1.6	20.8±1.6	63.9±2.4	36.1±1.8	−11.8±1.3	−0.6±2.1	−5.7±6.8	0.4±3.0
abcefi			44.2±3.1	24.0±1.1	73.9±1.5	41.3±1.1	−2.0±5.0	1.0±1.3	−12.5±6.0	−1.5±1.5
bcdfgh			55.7±3.0	27.2±1.8	75.2±1.0	40.9±1.8	−5.9±4.9	−2.5±1.3	−**15.5±4.6**	−2.7±3.1
bdefhi			59.4±2.9	25.4±1.0	78.4±1.2	43.1±1.1	−13.6±8.4	2.1±1.6	−**45.6±2.5**	−**15.9±1.9**

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