Science of the Total Environment 860 (2023) 160190

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Fauna access outweighs litter mixture effect during leaf litter decomposition

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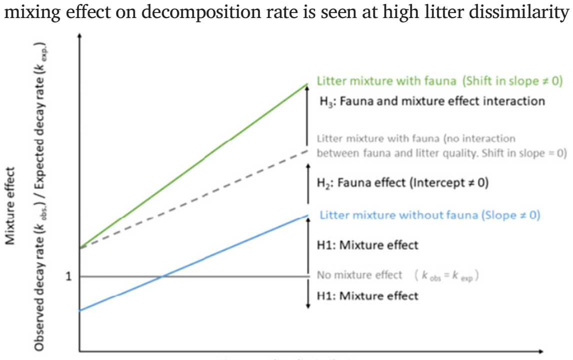
HIGHLIGHTS

- Litter quality, decomposers interact with each other and with the environment.
- Fauna accelerates litter mixture mass loss by 29.8 % on average.
- Fauna accelerates litter mixing effect via interact with decay length and initial quality.
- Litter mixing effect magnitude reduces as decay progresses.
- Species richness or dissimilarity of litter did not influence faunal effects on decay rates.

GRAPHICAL ABSTRACT

Conceptual framework of this study. The relationship between litter quality dissimilarity and relative mixing effect, (ratio of observed mass loss or decay rate to the expected). Hypothesis1 (H1) Mixing litters from different species will accelerate litter decomposition. This effect of litter mixture will increase with the differences in litter qualities in the mixture but will stay indifferent to litter species richness. H2 Presence of soil fauna will increase the rate of decomposition for both single species and litter mixtures and decomposition rate will be higher in presence of fauna than in absence of fauna. H3 The positive effects of litter dissimilarity and fauna size are non-additive, meaning that the largest mixing effect on decomposition rate is seen at high litter dissimilarity with both meso- and macrofauna.



ARTICLE INFO

Editor: Manuel Esteban Lucas-Borja

Keywords:
Biodiversity effects
Decomposers
Ecosystem function
Functional diversity

ABSTRACT

Decomposition rates of litter mixtures reflect the combined effects of litter species diversity, litter quality, decomposers, their interactions with each other and with the environment. The outcomes of those interactions remain ambiguous and past studies have reported conflicting results (e.g., litter mixture richness effects). To date, how litter diversity and soil fauna interactions shape litter mixture decomposition remains poorly understood. Through a sixteen month long common garden litter decomposition experiment, we tested these interaction effects using litterbags of three mesh sizes (micromesh, mesomesh, and macromesh) to disentangle the contributions of different fauna groups categorized by their size at Wuhan botanical garden (subtropical climate). We examined the decomposition of five

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http://dx.doi.org/10.1016/j.scitotenv.2022.160190
Received 10 August 2022; Received in revised form 9 November 2022; Accepted 10 November 2022
Available online 17 November 2022

Functional traits
Litter quality

single commonly available species litters and their full 26 mixtures combination spanning from 2 to 5 species. In total, 2325 litterbags were incubated at the setup of the experiment and partly harvested after 1, 3, 6, 9, and 16 months after exposure to evaluate the mass loss and the combined effects of soil fauna and litter diversity. We predicted that litter mixture effects should increase with increased litter quality dissimilarity, and soil fauna should enhance litter (both single species litter and litter mixtures) decomposition rate. Litter mass loss ranged from 26.9 % to 87.3 %. Soil fauna access to litterbags accelerated mass loss by 29.8 % on average. The contribution of soil mesofauna did not differ from that of soil meso- and macrofauna. Incubation duration and its interactions with litter quality dissimilarities together with soil fauna determined the litter mixture effect. Furthermore, the litter mixture effect weakened as the decomposition progresses. Faunal contribution was broadly additive to the positive mixture effect irrespective of litter species richness or litter dissimilarity. This implies that combining the dissimilarity of mixture species and contributions of different soil fauna provides a more comprehensive understanding of mixed litter decomposition.

1. Introduction

A substantial proportion of terrestrial primary production falls as litter and supports the detrital food web (Gessner et al., 2010) through their active role in decomposition (Cebrian, 1999). Litter decomposition drives nutrient and carbon cycling and thus helps in maintaining soil fertility, and thereby productivity, in terrestrial ecosystems (Cassart et al., 2020; Hobbie and Chapin, 1996; Patoine et al., 2017; Wardle et al., 1997). Climate, decomposers and litter quality are the key factors that control litter decomposition (Aerts, 1997; Fujii et al., 2018; Ostertag et al., 2022; Tan et al., 2021; Zhang et al., 2008).

Leaf functional traits, including structural and chemical traits, determine litter quality and, thereby, decomposability (Freschet et al., 2012). Mixing litters from different plant species can alter the litter mixture qualities compared to the average quality of the individual component species. Therefore, the diversity of plant litter might be an important determinant of decomposition rates in different ecosystems (Balvanera et al., 2006; Gessner et al., 2010; Patoine et al., 2017). The interactions between litter species on decomposition rates include transfer of inhibitory compounds or nutrients from one litter species to another (Handa et al., 2014; Lummer et al., 2012) and altered microclimate resulting from litter mixing (Wu et al., 2013). A number of studies have focused on the effects of litter diversity on decomposition by manipulating litter diversity at species level (Handa et al., 2014; Hättenschwiler et al., 2005). Mixed litter from different species results in different decomposition trajectories from what would be expected from the decomposition of individual component species, i.e., non-additive effects. However, no general pattern has been revealed to date on how litter mixture affects the decomposition process (Cassart et al., 2020). Some studies have reported that litter mixtures enhance the rate of decomposition overall (Gessner et al., 2010; Kaneko and Salamanca, 1999; Mori et al., 2020; Zeng et al., 2018; Zhang et al., 2022), while others showed opposite effects or no effect on the decomposition rate (Hoorens et al., 2010; Porre et al., 2020); the latter coined as additive effects of the component species (Njoroge et al., 2022). This uncertainty of litter mixture decomposition outcome could result from different microclimatic conditions within the experimental sites, traits of leaf litters under study, stages of decomposition (García-Palacios et al., 2013; Handa et al., 2014; Liu et al., 2020) and the lack of consideration of the role of invertebrate decomposers (Njoroge et al., 2022). The role of invertebrate decomposers can be studied experimentally by comparing litter mass loss in fine mesh litterbags excluding soil fauna with that in coarse mesh litterbags allowing soil fauna access.

Soil fauna plays an essential role in litter decomposition and their effect on single species litter decomposition has been widely studied (Hättenschwiler and Gasser, 2005; Schädler and Brandl, 2005; Wall et al., 2008). The role of soil fauna in decomposition could differ based on their classification by size (microfauna, mesofauna, macrofauna) (Menta, 2012), and trophic levels (prey and predators), while indirect effects need to be considered as well (Patoine et al., 2017). Soil fauna affects decomposition directly through feeding on the litter and fragmenting it (Hättenschwiler et al., 2005; Vos et al., 2013) and indirectly by exposing the litter to micro-organisms (Hector et al., 2000; Salamanca et al., 1998; Visser, 1985) or by grazing (for example by Collembola) on the decomposing fungi and bacteria (David, 2014). Most available studies have shown that soil fauna generally accelerates litter decomposition (García-Palacios et al., 2013; Schädler and Brandl, 2005; Wall et al., 2008; Yang and Chen, 2009). However, global models on litter decomposition lack the inclusion of the role played by soil fauna in decomposition, limiting our predictive power of global patterns of decomposition (Zhou et al., 2020).

Compared to the separate effects of litter mixing and soil fauna on decomposition, the interactions between litter diversity and soil fauna on litter decomposition have remained even more elusive. Previous studies have largely overlooked the fact that litter on the ground in most ecosystems comprises diverse species from which soil fauna select their diet (Gessner et al., 2010; Zhou et al., 2020). Very few studies have accounted for the effect of soil fauna during litter mixture experiments, limiting our understanding of the overall soil fauna effect and its interaction with litter diversity (Njoroge et al., 2022; Peguero et al., 2019; Tresch et al., 2019). Plant litter diversity and soil fauna might jointly affect the process of litter decomposition either positively or negatively (Handa et al., 2014; Kou et al., 2020; Sayer and Schafer, 2020; Vos et al., 2013; Yang et al., 2022). Fauna feeding activities and abundance dynamics could be changed depending on the composition of the mixture, hence altering litter mixture decomposition (Santonja et al., 2017; Zhang et al., 2022). Here, we argue that the current lack of pattern in the literature is at least partly because interactions between litter mixture decomposition and soil fauna may depend on which size category of soil fauna is considered; something that has largely escaped the attention of previous research. Moreover, to our knowledge limited studies have examined the interaction between litter dissimilarity and soil fauna in dictating the litter mixture effects (but see Patoine et al., 2020; Xiao et al., 2020).

To address this research gap, we aimed to answer whether and how the decomposition rates depend on the interactions between litter mixture species composition and soil fauna having access (categorized by size). Here, we propose a conceptual model (Fig. 1) that is built stepwise from the following hypotheses:

(i) Mixing litters from different species will change the decomposition of component single species litter. This effect of litter mixture will increase with the differences in litter qualities in the mixture (Barantal et al., 2014; Cassart et al., 2020; Vos et al., 2013) independently of litter species richness (Srivastava et al., 2009) (Fig. 1). We expect this because increased differences in litter quality will increase complementary resource utilization among decomposers (e.g., microorganisms and soil fauna). In addition, the average difference between each pair of litters in litter mixtures of different traits tend to decrease at high richness (beyond two species). This simply means that at high richness, the chance of finding high dissimilarity is smaller than at low richness.

(ii) The presence of soil fauna will increase the rate of decomposition for both single species and litter mixtures. The fauna effect on litter decomposition will also increase with an increase in fauna groups and differences in litter qualities (Fig. 1). We expect this outcome

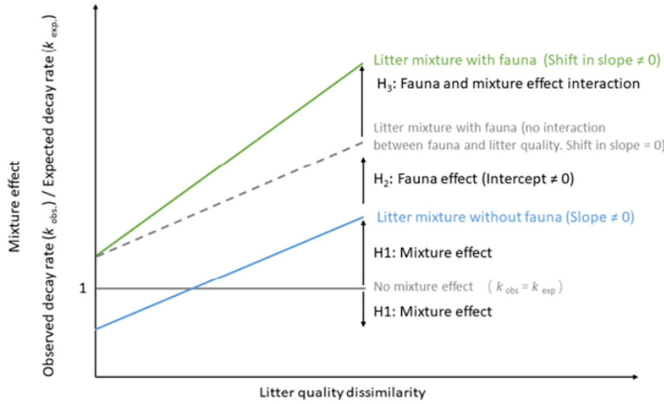

Fig. 1. Conceptual framework of this study. The relationship between litter quality dissimilarity and relative mixing effect, (ratio of observed mass loss or decay rate to the expected). Hypothesis1 (**H1**) Mixing litters from different species will accelerate litter decomposition. This effect of litter mixture will increase with the differences in litter qualities in the mixture but will stay indifferent to litter species richness. **H2** Presence of soil fauna will increase the rate of decomposition for both single species and litter mixtures and decomposition rate will be higher in presence of fauna than in absence of fauna. **H3** The positive effects of litter dissimilarity and fauna size are non-additive, meaning that the largest mixing effect on decomposition rate is seen at high litter dissimilarity with both meso- and macrofauna.

because different soil fauna groups might have different diet requirements, activities and some interactions with each other. For example, macrofauna could fragment and consume more litter than mesofauna. They may produce higher quality of feces which then might be preferred to litter itself by mesofauna or other decomposers or even lead to accelerated leaching (García-Palacios et al., 2013; Joly et al., 2020).

(iii) The positive effects of litter dissimilarity and fauna groups are non-additive, meaning that the larger mixing effects on decomposition rate are expected with higher litter dissimilarity for both meso- and macrofauna (Fig. 1). Litter mixtures composed of highly dissimilar litters are likely to increase the litter mixing effects as high litter dissimilarity could provide diverse microhabitats and sources of nutrients for microbes and soil invertebrates as opposed to more homogeneous mixtures (Cummins et al., 1989; Santonja et al., 2019b). In addition, when exposed to highly dissimilar litters in mixtures, complementary utilization of resources may occur for meso-fauna and macrofauna, which may stimulate further positive litter mixing effects (Vos et al., 2013).

To test these hypotheses, we carried out a common garden litter decomposition experiment examining the combined effect of litter species diversity (in short: litter diversity) and soil fauna of different size classes on litter decomposition in the early phase of decomposition.

2. Materials and methods

2.1. Litter collection

Freshly senesced leaves from five tree species were collected at the Moshan Park of Wuhan Botanical Garden in Wuhan, China (30°33′N, 114°24′E) during November 2019. The site has a typical subtropical monsoon climate. The average annual temperature is 16.3 °C and the average annual rainfall is 1214–1448 mm (Zhong et al., 2006). Previous studies have shown that gymnosperms and angiosperms (two major taxa of plants) decompose at different rates (Cornwell et al., 2008). This difference in decomposition appears mainly due to differences in quality (e.g., different types of lignin, i.e. guaiacyl lignin for gymnosperms and syringyl lignin for the angiosperms) (Cornwell et al., 2009). Therefore, since such differences in litter quality could affect the decomposers' effects, we decided to include species from both taxonomic groups to make our results more representative across a broad phylogenetic range. Thus, we selected two gymnosperms and three angiosperms species that are most abundant in Wuhan Botanical Garden. The two gymnosperms species were: *Taxodium distichum* (L.) Rich and *Pinus massoniana* Lamb, and the three angiosperms species were: *Quercus chenii* Nakai, *Liquidambar formosana* Hance and *Koelreuteria paniculata* Laxm. All litters were air dried in the laboratory and kept in air-tight boxes until July 2020, when they were weighed into litterbags and transported to the incubation site.

2.2. Litter quality measurement

For each litter species five 10 g subsamples were selected before the litterbag experiment. The leaves were ground to fine granules using a laboratory mill before chemical analysis in the laboratory. We measured the initial litter carbon (C), nitrogen (N), phosphorous (P), lignin and condensed tannin content for each subsample and the average per species was recorded. For the initial carbon and nitrogen measurements we used a MACRO Cube Elemental Analyzer (Elementa, Italy). We used an optical emission spectrometer to measure the initial P content after the samples were digested in the microwave digesting machine with concentrated nitric acid and hydrogen peroxide. Initial litter dry matter content (LDMC) was measured following Cornelissen et al. (2003). To measure initial lignin, we used Fibertec™ 2010 (FOSS Analytical AB, Sweden). Condensed tannin was measured my shaking the grounded samples with dimethylformamide and then after centrifuging ammonium citrate and amonia was added to the aliquot part of the supernatant. Spectrophotometer was used to determined the tannin content using a calibration curve prepared using tannic acid at 525 nm.

2.3. Decomposition experimental setup

Litterbags (20 cm × 15 cm) of nylon with three mesh sizes were used in this study: (1) micromesh (0.07 mm), permitting entry of microfauna only; (2) mesomesh (2 mm), permitting entry of micro- and mesofauna; and (3) macromesh (5 mm), permitting entry of micro-, meso- and macrofauna (Bradford et al., 2002). For the 2 mm and 5 mm litterbags the bottom layers were made of 0.5 mm mesh to prevent loss of the litter fragments from the litterbags (Barantal et al., 2014). In total, we had 31 litter treatments: five single species litters and all 26 possible combinations of two, three, four and five species. Each litterbag was filled with 10 g of air-dry litter and the species within each litter mixture were represented in equal proportions by mass. The incubation site was an open field initially covered with grass and weeds in the Guanggu Park of Wuhan Botanical Garden (30° 51′N, 114° 53′E). The collection site and the incubation site are within 11.3 km and therefore have similar climate. Five blocks (approximately 5 m × 5 m), separated from each other by approximately 1 m, were set up in a common garden and within each block, litterbags were placed on the surface and spread as flat as possible to maintain contact with soil during the entire decomposition period in the different incubation plots (Fig. S1). Each block served as one replicate for each treatment and harvest. To avoid the litterbags being carried away by wind, a large mesh net was laid on top of the litterbags after being placed on the soil surface. A total of 2325 litterbags were deployed at the five incubation blocks: 31 treatments × 3 mesh types × 5 replicates × 5 retrieval times. The retrieval times were at 1, 3, 6, 9 and 16 months after incubation. The incubation site was <500 m away from the laboratory, where we carried out the weighing so chances that there was litter fragmentation and loss as we transported the litterbags to the incubation site were minimal. Around the 14th month of the experiment there were some constructions nearby our common garden and this resulted to destruction of some of the litterbags, leading to the exclusion of 56 from our analysis. One of our main foci was on the fauna effect on litter decomposition, so after the onset of the experiment we collected soil fauna using pitfall traps set around the incubation plot (Fig. S6a). In addition, we checked for fauna in 15 cm soil depth and in the litter layer via handpicking and Tullgren funnel methods to confirm our assumption of soil fauna presence in our experimental plot (Fig. S6b).

At our last retrieval (after 16 months of incubation) we also extracted the soil fauna from the collected 5 mm and 2 mm litterbags using Tullgren funnels (Fig. S6c)), identified them using a light microscope, and classified them into taxonomic groups up to order. We also recorded the abundance of each order within the litterbags at the end of the experiment (Table S1).

During each retrieval, litterbags were carefully transported to the laboratory where they were gently brushed to remove soil and other external particles. When there was a high amount of soil attached to the litter (e.g., especially in the 9th and 16th month retrieval) we gently rinsed the litter samples with tap water in 0.5 mm mesh size trays to remove the soil particles. The remaining leaf litters were then oven dried at 60 °C to a constant mass. Oven-dried litter was weighed to the nearest 0.01 g to determine its mass loss.

3. Data analysis

The average concentration of C, N, P, lignin, condensed tannin and LDMC in litter mixtures were calculated as the average concentration in the component single species in the mixture (Vos et al., 2013) using the following equation:

$$\textit{Mean trait value}\ (tv) = \sum_{i=2}^{5} \frac{tv_{spi}}{i}$$

Where tv is the initial value for C, N, P, lignin or condensed tannin concentration or LDMC. Initial litter quality dissimilarity among component litter species in the mixture was estimated as the Euclidian distance between each pair of litter species in the mixture using the function *vegdist ()* from the package vegan (Oksanen et al., 2020). Only C, P, lignin, condensed tannin and LDMC were used in calculating the Euclidean distance since N was highly collinear to P and condensed tannin while C:N was highly collinear with C and N. Prior to calculating the Euclidian distance, the initial litter quality measurements were standardized so that they had a mean of zero and a standard deviation of one (Santonja et al., 2019a). For litter mixtures consisting of more than two species, we calculated the average Euclidian distance of all pairs of the component species in the mixture (Hättenschwiler and Jørgensen, 2010).

The mass loss during the incubation period was calculated as a percentage of the initial litter dry mass for each litter treatment remaining at the time of harvest.

$$ML = \frac{M_{initial} - M_{final}}{M_{initial}} * 100$$

$M_{initial}$ being the initial dry mass of leaf litter and M_{final} being the final leaf litter dry mass at the time. To calculate the estimated annual rate of decomposition (k) for the single and mixed species litter we used the following equation (Olson, 1963)

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

Where t is the incubation time in years, M_0 is the initial mass in the beginning of the experiment, and $M_{t\ is}$ the mass loss at time t.

To determine the effect of litter diversity on litter decomposition, we calculated the relative mixing effect (MER) on decomposition. This was done by comparing the expected mass loss ($M_{expected}$) based on the mass loss of the single component species to the observed mass loss ($M_{observed}$) of the litter mixture:

$$MER = \frac{M_{observed}}{M_{expected}}$$

following the methods by Pretzsch et al., 2010; Grossman et al., 2020. Expected mass loss was calculated based on the single species litter in 0.07 mm mesh size that did not permit mesofauna and macrofauna access to the litter using the following equation:

$$\text{Expected mass loss}\ (\%) = \sum f_i M_i$$

M_i is the percentage mass loss and f_i the mass proportion of each single species litter in the litter mixture in the 0.07 mm mesh size litterbags. Values >1 indicate accelerated decomposition for the mixed litter whereas values <1 indicate decelerated decomposition rate compared to the expected rate of decomposition based on the component single species litters. We calculated a 90 % confidence interval for the mean value of each species mixture (five replicates per mixture) then using Student *t* distribution to determine which litter mixtures deviated from the expected mass loss (Grossman et al., 2020). We considered the decomposition of litter mixtures to deviate from the expected rates when the value of 1 was not included in the confidence intervals. To test the effect of soil fauna on litter mixture effect during decomposition, we compared the relative mixing effect in the 0.07 mm mesh sizes to that one of 5.0 mm and 2.0 mm mesh size litterbags. The difference between relative mixing effect in the 0.07 mm mesh size and the relative mixing effect in 5.0 mm and 2.0 mm mesh size was considered as the fauna effect (Fig. 1).

The relationship between our dependent variable (relative mixing effect) and trait dissimilarity, number of species and litterbags mesh size, respectively, was examined by linear regression. In cases where the response variable data was not normally distributed, we log transformed the data to make it normally distributed before running the regression. We used Pearson correlation to test (*cor ()* function) for correlations among the variables with a threshold of 0.70 considered as highly correlated (Makkonen et al., 2013). When two variables exhibited ≥ 0.70 Pearson correlation, then only one of them was included in our final model. We implemented linear mixed models with *lme4* package (Bates et al., 2015) to test the factors that best explained variations in the relative mixing effect. Time, trait dissimilarity, number of species and litterbags mesh size were used as fixed effects and litter combination, harvests and the five incubation plots were the random effect terms ((1|Block/Block_harvest) + (1|Litter_combinations)). We used a random intercept model. We plotted the standardized residuals against the fitted values to check homoscedasticity, and normality of the residuals in our models. To reach an optimal model for our data from the initial maximum model we subtracted variables one variable at a time starting with the most non-significant interactions. In doing so, we used likelihood test ratio and we were careful not to violate the principle of marginality (Dossa et al., 2021). We checked for conditional r^2 (variance explained by both fixed and random terms) and marginal r^2 (variance explained by the fixed effect terms of the model) to assess the model's performance using *r.squared GLMM* function from *MuMin* package (Barton, 2020). To compare the pairwise differences among mesh sizes we applied *emmeans* function from emmeans package (Russell et al., 2022).

4. Results

4.1. Trait values of litter across species and single species decomposition

The litter from 5 tree species differed in initial traits (Table 1). After sixteen months, mass loss of single species litter was the highest for *K. paniculata* (58.52 %), followed by *L. formosana* (56.32 %) *T. distichum* (54.41 %), *P. massoniana* (40.06 %) and was the lowest for *Q. chenii* (38.55 %). Mass loss and decomposition rate in the five harvest times was higher in the three fast decomposing species (*K. paniculata, L. formosana* and *T. distichum*) and always lower in the slow decomposing species (*Q. chenii* and *P. massoniana*) (Fig. S3 and S4).

4.2. Litter mass loss and litter mixture effect

Mass loss for the litter mixtures increased with the incubation time and after sixteen months the highest mass loss was 59.21 % in the mixture composed of the three fast decomposing litter species (*K. paniculata*,

Table 1
Litter initial traits of the five tree species (Mean ± SE). Different letters represent significant differences between species.

Species	Nitrogen (N) %	Carbon (C) %	Phosphorus (P) %	C:N	Leaf dry mass content (LDMC) g/g	Lignin %	Condensed tannin %
Pinus massoniana	0.66 ± 0.03b	51.15 ± 0.42b	0.027 ± 0.004b	77.50a	0.68 ± 0.01a	21.15 ± 1.93ab	2.6 ± 0.08a
Taxodium distichum	0.75 ± 0.07ab	46.45 ± 0.22bc	0.105 ± 0.06ab	61.93a	0.41 ± 0.02b	34.7 ± 4.02a	2.34 ± 0.1a
Quercus chenii	0.88 ± 0.04a	48.95 ± 0.54c	0.116 ± 0.01a	55.63b	0.49 ± 0.01ab	25.9 ± 3.3ab	7.19 ± 0.26b
Liquidambar formosana	0.83 ± 0.03a	40.55 ± 0.56a	0.095 ± 0.05a	48.86ab	0.58 ± 0.11ab	31.15 ± 0ab	5.77ab
Koelreuteria paniculata	1.10 ± 0.16c	45.57 ± 5.84c	0.26 ± 0.05c	41.42b	0.38 ± 0.01b	39.40 ± 1.12b	10.33 ± 1.2b

L. formosana and *T. distichum* mixture) and the lowest mass loss was 40.76 % litter composed of slow decomposing litter species (*Q. chenii* and *P. massoniana*, *T. distichum* mixture). Species richness as a single predictor did not have a significant effect on litter mass loss. However, when we compared the mean mass loss per species richness level, the averaged mass loss for all mixtures was highest in mixtures made of three species throughout the experiment duration apart from the sixteenth month. Averaged rate of decomposition was also higher in mixtures made up of three species at the end of the experiment period (Fig. S5). Litter mass loss and decomposition rate in 2.0 mm and 5.0 mm litterbags was higher than in 0.07 mm litterbags irrespective of the number of species in the litter. The interaction between species richness and the mesh size was non-significant. Litter quality dissimilarity did not have a significant effect on litter mass loss ($P = 0.14$).

On average the observed litter mass loss for litter mixtures was higher than the expected mass loss. However, the relative mixing effect (MER) for most mixtures varied with incubation duration. The relative mixing

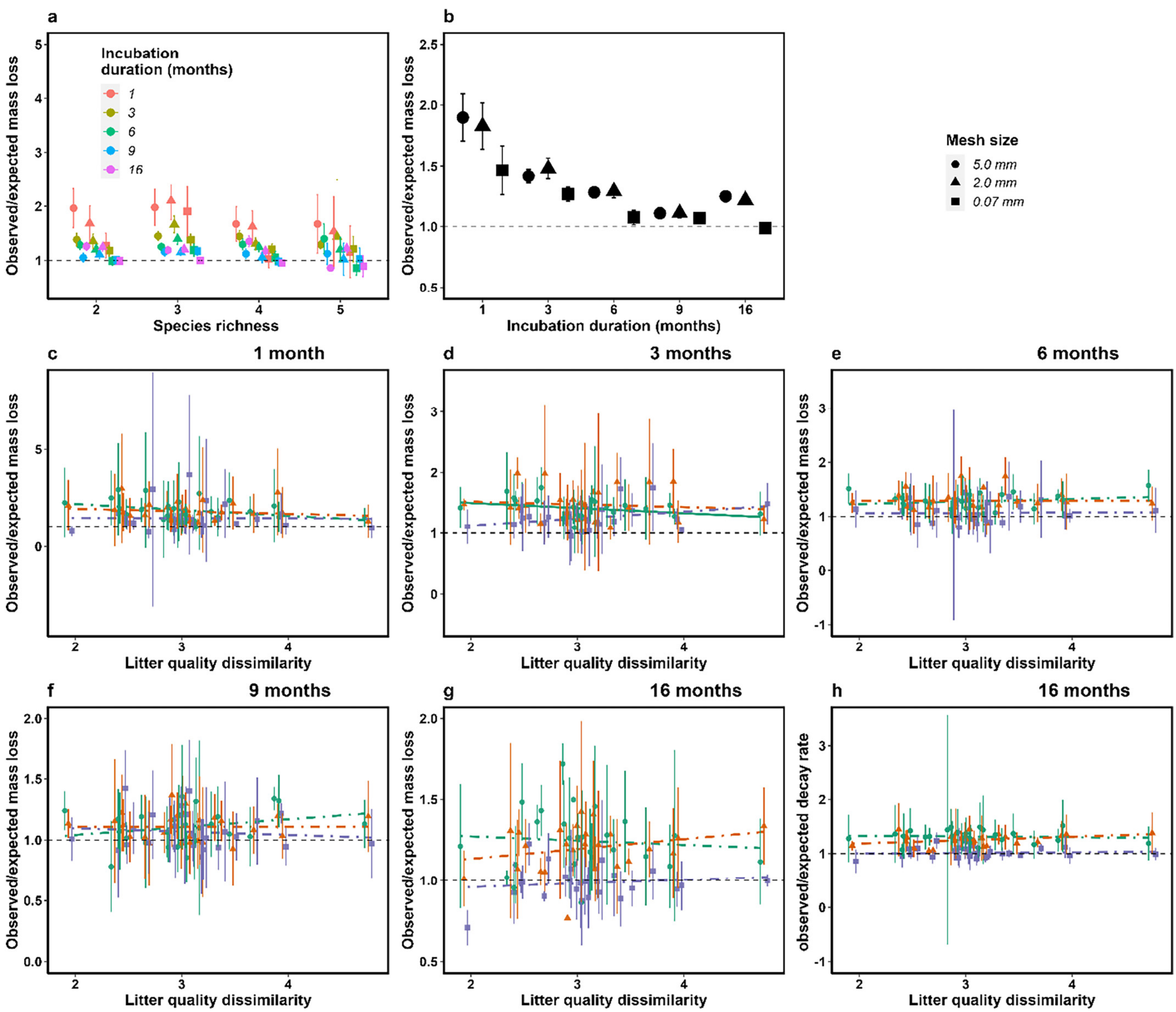

Fig. 2. Relative mixing effect of litter mixtures and its relationship with a) species richness b) incubation duration. c-g show the relationship of relative mixing effect with litter quality dissimilarity after one, three, six, nine and sixteen months of litterbag incubation, respectively. h) shows relative mixing effect based on decay rates (*k*). Values above one (> 1) indicate that mixing litters enhances litter decomposition while values below one (< 1) indicate that mixing litters diminishes decomposition of litter. For a and b when the error bar crosses the horizontal dashed line, mixing litter does not affect decomposition. The dashed lines in c-h represent the non-significant slope for each fauna group.

effect was higher in the initial stages of decomposition (< six months) and slowed down in the later stages of decomposition (Fig. 2b). Increasing species richness in the litter mixtures did not result in a stronger relative mixing effect in the mixture (non-significant regression slope). However, the mean MER per species richness level increased from two species to three species litter mixtures and then dropped in mixtures with four and five species (Fig. 2a). The overall relative mixing effect across all litter treatments varied across the three mesh sizes ($F_{2,1656} = 47.93$, $P < 0.001$) (Fig. 2a and b). Average MER in 5.0 mm mesh was significantly different from that in 0.07 mm mesh ($P < 0.001$) but not from that in 2.0 mm mesh. The average MER in 2.0 mm mesh size was also significantly different from 0.07 mm mesh size ($P < 0.001$). Litter quality dissimilarity did not predict the litter mixture effects as we had hypothesized but its interaction with time was significant (Fig. 2c-h, Table 2). The selected best linear mixed model however, only explained around ~26 % of the observed variance (r^2c) in relative mixing effect. Interestingly also the r^2c was triple the r^2m implying that the random factors (litter combination, block, and harvests) explained more variation in our model.

4.3. Fauna effect and fauna interactions with litter mixtures

The decomposition rate (k) after sixteen months significantly varied with the litterbag mesh size and was higher in 5.0 mm mesh size and lowest in 0.07 mm mesh size litterbags at all species richness levels (Fig. S5). Similarly, litter mixture mass loss was significantly different between the three mesh sizes. Litter mixtures in 0.07 mm mesh had the lowest mass loss with an average of 43.9 % while the 2.0 mm and 5.0 mm mesh size litterbags had an average of 53.0 % and 54.9 %, respectively after sixteen months. On average soil fauna access (both mesofauna and macrofauna) to litterbags accelerated mass loss by 29.80 %. Mass loss in the 5.0 mm and 2.0 mm did not deviate much from each other (Fig. 3a). Generally, litter mass loss was higher for 2.0 mm and 5.0 mm mesh compared to the 0.07 mm mesh (Fig. 3b and c). Soil fauna enhanced litter mixing effect in that relative mixing effect was higher in 2.0 mm and 5.0 mm mesh size than in 0.07 mm throughout the incubation period and species richness levels (Fig. 2a and b). The litterbags mesh size was a significant predictor of the relative mixing effect (Table 2).

5. Discussion

Through this common garden experiment, we aimed to disentangle the effect of soil fauna from the effects of litter mixture on litter decomposition as well as the contribution of different soil fauna groups in terms of body size. We expected, on one hand, a complementary utilization of resources by decomposers which would be depicted by an increase of decomposition rates along a gradient of litter quality dissimilarity in litter mixture irrespective of species richness. On the other hand, we hypothesized that access of soil fauna would enhance litter decomposition regardless of litter types (single species litter or litter mixtures). We demonstrated that inclusion of soil fauna in the process of leaf litter decomposition generally accelerates decomposition both in single species litter and in litter mixtures. We also showed that soil fauna inclusion in litter mixtures enhances litter mixing effect during the decomposition process. Additionally, we showed that higher initial litter quality dissimilarities do not necessarily result in increased litter mixture effect during the process of decomposition. Furthermore, our results highlight the impact of decomposition duration on litter mixture effect; the litter mixtures effect weakens as incubation duration progresses.

5.1. Litter mixing effect

In line with our first hypothesis, mixing leaf litters from different species resulted in an overall accelerated decomposition rate. This corroborates results from global syntheses by Liu et al. (2020), Kou et al. (2020), Xiao et al. (2020) and Mori et al. (2020) who reported that, litter mixing mostly enhances decomposition rates. We did not find any significant relationship between litter quality dissimilarity and litter mixture mass loss. This observation corroborates an observation by Frainer et al. (2015) in a three-month long stream decomposition experiment involving eight broadleaves species and all their possible pairwise combination using two mesh sizes (0.5 mm and 10 mm). They reported that litter trait dissimilarity did not predict litter decomposition rate. Contrary to our expectation, litter quality dissimilarity did not have a significant effect on the relative mixing effect but its interactions with time had a significant influence on the relative mixing effect. This result implies that although the relative mixing effect during decomposition does not vary with changes in the quality dissimilarity of its constituent litters the interaction of quality dissimilarity and time has a significant effect on relative mixing effect. This observation confirms that of Porre et al. (2020), who reported that litter quality dissimilarity without other factors failed to predict the interactions that occur during litter mixing. As predicted, species richness did not have a significant effect on the litter mixing effect. This suggests that in litter mixtures, species composition, via differences in their litter traits, rather than species richness represents a better predictor of litter mixing effect during the process of decomposition (Cassart et al., 2020; Wu et al., 2013). However, when we considered the average relative mixing effect (MER) per species richness level, we observed that different levels of species richness resulted in a positive relative mixing effect (only up to three species). Beyond species richness of three in mixtures, no further increase in mixing effect was observed. The apparent saturation of MER beyond three species may partly be explained by the average litter dissimilarity for the various species pairs in the mixture always being moderate. Indeed, we found that the litter dissimilarity index peaked at 3 (Fig. S7). In addition, beyond three species the surface area of interactions between the species of each pair within the litterbags (and in multi-species litter mixtures in general) is greatly reduced; hence any non-additive effects on decomposition between species pairs would be diluted in litter mixtures with more than three species.

5.2. Soil fauna effect on litter mixtures decomposition

In support of our second hypothesis, we observed that litter mass loss was higher in litterbags that allowed meso- and macrofauna access regardless of litter types (single species or multiple species mixtures). This observation corroborates previous studies that reported increased rates of decomposition in litter when litter mixtures allowed access of soil fauna (Santonja et al., 2019b; Vos et al., 2011; Wall et al., 2008; Zhang et al., 2022). We observed that species richness had no significant effect on litter mass loss. Furthermore, the interaction between species richness and soil

Table 2
Linear mixed model of the best sets of variables explaining relative mixing effect (log transformed) during the sixteen-month decomposition period. Blocks, harvests and itter combination were used as the random term in the linear mixed model. DF is the degree of freedom. r^2_m is the marginal r^2 which is the variance explained by the fixed effect terms of the model while r^2_c is the conditional r^2 which is the variance explained by both fixed and random terms of the model. We obtained p-values by Satterthwaite's method using *lmerTest* R package. P values indicated in bold are significant.

Variable	Random effects	Fixed effects	Sum of squares	Numerator (DF)	Denominator (DF)	F value	P values
Relative mixing effect	(Block/ Harvest) + (Litter combination)	Litter quality dissimilarity	0.27	1	53.71	2.11	0.15
		Mesh size	12.70	2	1656.06	47.93	**< 0.001**
		Time	1.18	1	184.63	8.95	**< 0.001**
$r^2m = 0.08, r^2c = 0.26$		Time: Litter quality dissimilarity	0.54	1	1665.71	4.13	**0.04**

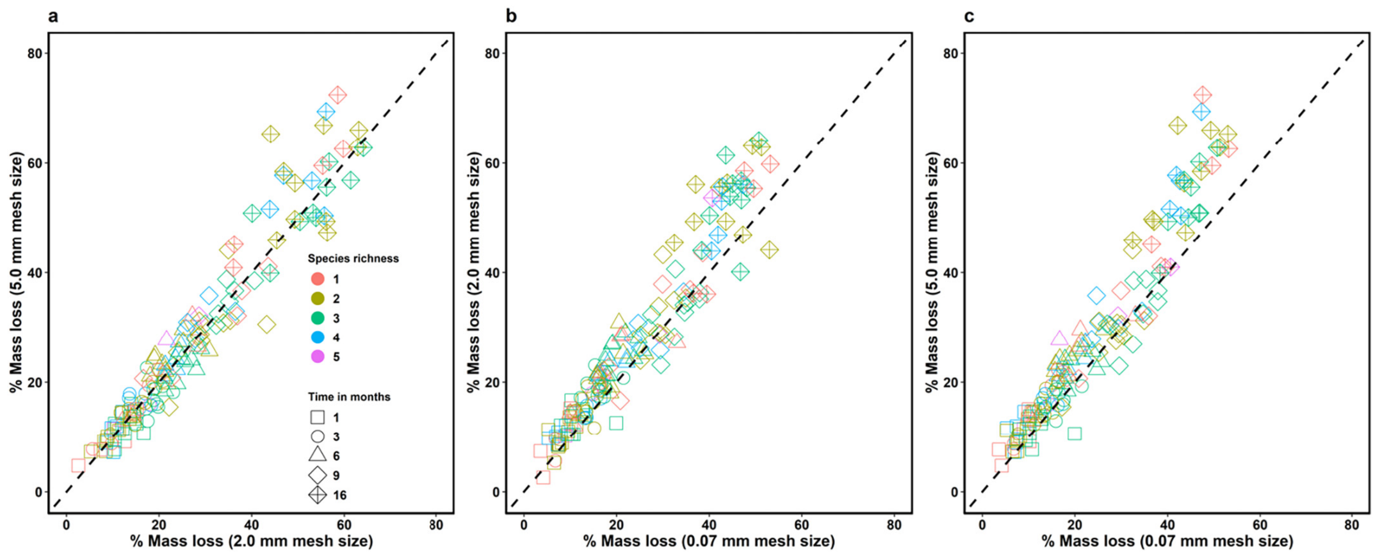

Fig. 3. Litter mass loss for single species and litter mixtures in the 0.07 mesh size litterbags against b) litter mass loss in 2.0 mm and c) litter mass loss in 5.0 mm mesh. a) Mass loss in 2.0 mm against 5.0 mm mesh. Values above the dashed line (1:1 line) indicate that the inclusion of mesofauna (in a) and both mesofauna and macrofauna (in b) increases decomposition mass loss while values below indicate that fauna inclusion reduces litter mass loss. Values above the dashed line indicate that litter decomposes faster when macrofauna and mesofauna are both present while values below the dashed line indicate that litter decomposes faster when only mesofauna is present.

fauna was not significant in modulating litter mass loss in the mixture. This result contradicts those of Hättenschwiler and Gasser (2005) who observed that litter species richness together with soil fauna interactively determine decomposition of litter in ecosystems. The presence of soil fauna also contributed to significant positive variations in the relative mixing effect when the two groups (mesofauna and macrofauna) of fauna were included in the litter mixtures. This reveals that soil fauna do not only increase litter mass loss but also contribute to modulating the outcomes of the litter mixing effect in ecosystems. Recent studies have also concluded that inclusion of these fauna groups in litter decomposition experiments modify the decomposition of litter species within mixtures (Zhou et al., 2020). Furthermore, three meta-analysis on global decomposition have revealed that inclusion of soil fauna during decomposition of litter mixtures often results in accelerated decomposition for the litter mixtures (Kou et al., 2020; Liu et al., 2020; Njoroge et al., 2022). Increasing litter quality dissimilarity increases complementarity of resources for soil fauna (Barantal et al., 2014; Heemsbergen et al., 2004), which we expected to increase the fauna effect on litter mass loss.

5.3. Soil fauna and litter mixture interaction

The litter mixture effect was reduced as decomposition duration progressed and varied with the mesh size throughout the decomposition period. Perhaps, the high initial dissimilarity among components species in the mixtures gets reduced and thus might not attract as many fauna at later stages as decomposition progresses. Initial litter traits may converge to a common poor quality (after depletion of nutrients) in the mixtures hence retarding litter mixture effect as decomposition progresses (Butenschoen et al., 2014). Similar results have been reported on the decline of litter mixing effect magnitude and frequency in some previous studies (Canessa et al., 2022; Lecerf et al., 2011; Wu et al., 2013). Moreover, it is probable that soil fauna consumption rates are linked to nutrient contents and dynamics within the litter (Joly et al., 2020). For example, for a given nutrient requirement of their diet, fauna may consume more biomass in the presence of poor litter quality than in the presence of rich litter quality (Swan and Palmer, 2006a). This is coined as compensatory feeding by fauna (Jochum et al., 2017). Furthermore, a study by Swan and Palmer (2006b) reported that fauna feeding rate was relatively high in solely low quality litter of American sycamore (*Platanus occidentalis*). However, when the American sycamore was mixed with other species litter, which increased the overall mixture litter quality, the fauna feeding rate on the American sycamore was greatly reduced and thereby reduced the overall decomposition of the mixture as a whole. This phenomenon has been coined as preferential feeding by soil fauna. Preferential feeding by soil fauna dominates the initial stages of decomposition when the litter dissimilarity is high, but as decomposition progresses and nutrients are leached out the litter quality reduces and compensatory feeding by fauna dominates. Preferential feeding in the early stages of decomposition and compensatory feeding by soil fauna on the low quality litter in the later stages of decomposition of litter mixtures could explain the reduced soil fauna effect as litter quality dissimilarity increases and the positive interactions between litter quality dissimilarity and incubation duration.

6. Conclusion

Here, using a common garden experiment with manipulative treatments, we show that soil fauna accelerates the rate of litter decomposition over sixteen months for both single species litter and litter mixtures. Furthermore, decomposition duration and also its interactions with litter quality dissimilarity modulates the litter mixing effect. Species richness in litter mixtures is also shown to accelerate litter decomposition, but there is a three-species limit beyond which further increase in the number of species in the mixture has no impact on decomposition and litter mixing effect. We also demonstrate that species composition rather than species richness holds higher predictive power of litter mixture effects. Our results emphasize the importance of soil fauna, decomposition duration and their interactions in shaping litter mixtures decomposition outcomes. For a better understanding and good predictions in global decomposition models, the soil fauna contribution along with the interactions between species diversity (trait dissimilarities) in controlling litter mixtures decomposition need to be considered (Canessa et al., 2022; Joly et al., 2020).

CRediT authorship contribution statement

Conceptualization: DMN, GGOD, JZ contributed equally to the conception of experimental design and methods; Data curation: DMN, GGOD, JZ; Formal analysis: DMN, GGOD, JZ, KT (DMN, GGOD, JZ contributed equally); Funding acquisition: JZ, GGOD; Investigation: DMN LY, XL;

Methodology: DMN, GGOD, JZ; Project administration: JZ, GGOD; Supervision: JZ, GGOD; Validation: JZ, GGOD, JHCC; Visualization: DMN, GGOD, JZ; Roles/Writing - original draft; Writing - review & editing: DMN, GGOD, JZ, LY, XL, KT, DAS, JHCC; All authors contributed critically to the drafts and gave final approval for publication.

Data availability

Data and analyses code for this paper are accessible at the public repository https://github.com/dossag/Fauna_outweighs_mixture_effects_SOTEN.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The study was supported by the Knowledge Innovation Program of Wuhan - Basic Research (2022020801010166) and a research grant from Wuhan Botanical Garden, Chinese Academy of Sciences (Y9559701). The project was supported by Open Funding from CAS Key Laboratory of Tropical Forest Ecology (22-CAS-TFE-06). This work benefitted financial support from the National Natural Science Foundation of China (NSFC) via grant (31850410488) to GGOD. In addition, GGOD was supported by Yunnan Province Government for Talents Program (E1YN101B01), Zhi Hui Yunnan Program (202203AM140024), and young international staff Chinese Academy of Sciences (CAS) president international fellowship initiative (PIFI) grant (2019FYB0001). LY was supported by Open Funding from CAS Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences (E0520205). We also acknowledge Prof. Ming-Xi Jiang, Chao-Chao Deng, Fan Li, Xin-Yi Gong, Kang Ji, Dang-Jun Wang, and Yong Zheng for their help in the initial stages of the experiment setup and laboratory work. We would like to thank the Institutional Center for Shared Technologies and Facilities of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences for their assistance with analyzing chemical contents of litter used in this experiment. We acknowledge Dr. Robert Bagchi from University of Connecticut for giving his expert opinion on the experimental design and statistics. We are thankful to the editor and reviewers for the constructive comments on earlier version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.160190.

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