Species and genetic diversity affect leaf litter decomposition in subtropical broadleaved forest in southern China

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Abstract

Aims
Litter decomposition is a fundamental process within ecosystem functioning, and it is largely dependent on the biodiversity of ecosystems. We explored the effects of species diversity and genetic diversity of litter on the litter decomposition rate.

Methods
We used laboratory microcosms to determine whether species diversity and genetic diversity and their interaction affect leaf litter decomposition. We set up 8 treatments containing 1, 2, 4 diversity levels of four broad-leaf species (Anaphyllum fortunei, Idesia polycarpa, Cinnamomum camphora and Daphniphyllum oldhamii) both in species and genetic sense. Totally 246 microcosms containing same amount of soil and litter of prescribed diversity treatment were stored in the dark at 25°C for 12 weeks.

Important Findings
The effect of litter species diversity on litter decomposition was largely dependent on species composition of the litter mixture in terms of species identity. Overall, the decomposition rate increased linearly with the richness of seed family when the species identity was disregarded. However, no interactive effect of species diversity and genetic diversity on mass loss was detected. The litter decomposition rate was found to be unrelated to the initial carbon (C), whereas it was negatively correlated with the initial total nitrogen (N) and N:P ratio. However, the regression curves of the litter decomposition rate against the total P and C:N ratio displayed quadratic parabolas opening upward and downward, respectively. This study demonstrated how species and/or genetic diversity and the stoichiometry of litter per se affect litter decomposition. Further studies should be performed in the long term to ascertain how such effects operate and how they change during the decomposition process, particularly in response to varying composition and diversity of standing plants in the environments.

Keywords: C:N, litter chemistry, mass loss rate, microcosm, N:P, seed family

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INTRODUCTION

Due to increasing human activities, loss of biodiversity has become an increasingly severe ecological problem globally; thus, the relationship between biodiversity and ecosystem functioning has become a popular theme within ecological studies (Balvanera et al. 2006; Cardinale et al. 2012; Naem et al. 2012; Peng et al. 2017). A large number of articles have been published focusing on the consequences of biodiversity loss on ecosystem functions such as primary production, decomposition and biogeochemical cycles (Gessner et al. 2010; Hooper et al. 2012; Huang et al. 2017). As fundamental ecosystem function, decomposition is a complex process involving interactions between physical, biological and chemical processes. The processes operating within litter decomposition are largely dependent on climate, litter quality, plant functional traits and the detrital food web (Aerts 1997; Coûteaux et al. 1995; Li et al. 2004; Swift et al. 1979). On the global scale, climate is the best predictor of the litter decomposition rate (Bailey et al. 2014; Boyero et al. 2011; Hines et al. 2014), whereas litter quality has a much higher predictive value at a local scale (Dangles and Malmqvist 2004; Sariyildiz 2015; Sariyildiz and Kucuk 2008).
Litter chemistry varies both at a species and genotype level, and it is of great importance for litter decomposition (Cornelissen et al. 2003; Hättenschwiler and Jörgensen 2010; Koerselman and Meuleman 1996; Madritch et al. 2006; Talbot and Treseder 2012). However, plant diversity influence litter decomposition not only by altering litter chemistry, but also by modifying the microclimate and soil decomposer community (Jia et al. 2015; Rousk et al. 2015; Wang et al. 2014); thus, there is an absence of a unidirectional response. The underlying mechanisms leading to the observed effects remain unclear (Gessner et al. 2010; Hättenschwiler et al. 2005). In field experiments, it is difficult to separate the effects of microclimate from those of other factors on litter decomposition, such as litter chemistry and the decomposer community; however, these effects might be better separated under controlled conditions, e.g. in a microcosm study.

To date, previous field studies on the relationship between biodiversity and litter decomposition used the litterbag method and reached conclusions falling exclusively into three categories: (i) synergistic effects (Mao and Zeng 2012; Marco et al. 2011; Zhang et al. 2014); (ii) antagonistic effects (Dangles and Malmqvist 2004; Prescott et al. 2000) and (iii) purely additive effects (Smith and Bradford 2003; Lecerf 2007; Scherer-Lorenzen et al. 2007). However, these effects were detected mainly from the experiments focusing on species diversity, whereas the effects of genetic diversity on litter decomposition remain poorly understood. In fact, genotypes of a single plant species usually differ in traits affecting litter decomposition (Madritch et al. 2006; Schweitzer et al. 2004, 2005; Treseder and Vitések 2001); therefore, non-additive effects of genotype mixture can act in parallel to those of plant species mixtures (Schweitzer et al. 2005). A considerable portion of the underlying mechanism may comprise the mediation of decomposers, as leaf litter from different genotypes may support different decomposers (resource specialization hypothesis), or decomposer diversity can increase due to their greater number of individuals in diverse leaf litter (more individuals hypothesis; Crutsinger et al. 2006). Nevertheless, few studies have addressed the interactive effect of species diversity and genetic diversity on litter decomposition.

In the present study, we investigated whether and how species diversity and genetic diversity independently and/or interactively influence the decomposition of leaf litter. Specifically, we addressed the following unknowns: (i) how the leaf litter decomposition rate responds to the species diversity and genetic diversity of litter per se; (ii) whether interaction between species diversity and genetic diversity occurs during leaf litter decomposition and (iii) the extent to which litter decomposition is affected by litter ecological stoichiometric traits.

MATERIALS AND METHODS

Study site

The experiment was performed at the study site of the BEF-China project near Xingangshan, Daxing, Jiangxi Province (29.08°–29.11°N, 117.90°–117.93°E), China. The region is characterized by a subtropical monsoon climate, and the mean annual temperature and precipitation are 16.7°C and 1821 mm, respectively (Bruehlheide et al. 2011). To initiate the project, the forest was artificially planted in 2009 and 2010, during which tree diversity (both at species and genetic level) was manipulated to study the relationship between tree diversity and ecosystem functioning and services (Bruehlheide et al. 2014). In total, there are 556 plots in the two discrete sites. Each plot has an area of 666.7 m² (25.8 × 25.8 m), in which 400 trees were planted (arrayed in 20 lines × 20 columns), with a distance of 1.29 m between adjacent trees in the same line or column (Bruehlheide et al. 2014). Before tree planting, 24 plots were randomly chosen and assigned as genetic plots, used to study the effects of genetic diversity as well as species diversity. In these genetic plots, the trees of four species (Alniphyllum fortunei, Cinnamomum camphora, Daphniphyllum oldhamii and Idesia polycarpa) were planted, with two-species diversity levels (one or four species) interacting with two genetic levels (one or four seed families; Zeng et al. 2017).

Collection of leaf litter and soil

During late October 2013, senescence leaves of each seed family of the four species (A. fortunei, C. camphora, D. oldhamii and I. polycarpa) were collected from the 24 genetic plots, and then were transported back to the laboratory and oven-dried at 65°C to a constant weight to be used later in a subsequent laboratory experiment. When collecting leaf litter, a certain amount of soil was concurrently collected from the upper 10 cm of the mineral soil surface outside, but nearby the BEF-China plots, transported to the laboratory and air-dried, sieved through a 2 mm mesh, and stored for use as substrate in the subsequent microcosm decomposition experiment. The pH value of the soil was around 4.54, and the C:N was ~10.55 (Scholten et al. 2017).

Decomposition experiment in the laboratory

We used 246 round containers composed of paper (3 cm in diameter, 6.5 cm in height), as litter decomposition microcosms, to determine whether diversity of leaf litter affects litter decomposition. We established three levels for both species and genetic diversity, containing one, two and four species and seed families, respectively, resulting in eight combinations, whereas for mono- and two-species treatments, multiple species × seed family combinations were adopted (Table 1). Each species × seed family combination was replicated six times, resulting in six blocks, with each block assigned to a biochemical incubator (LRH-70, Shanghai Yiheng Technical CO., LTD). All litter samples were cut into 5 mm fragments to facilitate mixing. For each replicate, 0.78 g litter was put on the surface of 25 g (dry weight) soil in a microcosm with a contacting area of 30 cm². The microcosms were incubated in the dark at 25°C for 12 weeks, and were harvested every four weeks. When
we harvested the microcosms, the litter pieces were collected, cleaned, oven-dried (65°C, 48 hours) and weighed, then the pieces were placed into the former containers. The relative humidity in all the microcosms was maintained at 90–100% by regularly spraying deionized water into all the microcosms.

To facilitate the subsequent reference to seed families and their mixture, we used a coding system in all following text, tables and figures. Seed family is denoted by the initial letter of species name followed by a hyphen and an Arabic number (assigned when planted in the nursery). The mixture of seed families of a single species was denoted by the initial letter of species name followed only by an Arabic number indicating the number of seed families involved.

Chemical analysis of leaf litter

The total carbon (C) concentration of leaf litter was determined by potassium dichromate oxidation titration (Lavian et al. 2001), the total N content was determined with the Kjeldahl method, and the total P was determined by the Mo-Sb colorimetric method.

Data analysis

All data were tested to satisfy normality assumptions using the Kolmogorov–Smirnov test, and non-normal data were log transformed. The litter decomposition rate was determined with a negative exponential equation (Olson 1963):

$$x_t / x_0 = e^{-kt}$$

where $x_0$ is the initial litter mass, $x_t$ is the litter mass remaining at time $t$, and $k$ is the litter decomposition rate ($a^{-1}$).

Expected mass loss of litter mixtures was calculated as the mean mass loss of each component in the single family treatments. A paired student’s t-test was used to test whether observed mass loss differed from expected mass loss in the mixed treatments. We used repeated measures analysis of variance (ANOVA) to test for the effects of species diversity, genetic diversity, litter components and block and harvest times (Schmid et al. 2017). We used a one-way ANOVA to compare differences between the litter compositions and litter chemical content of each seed family. All analyses were performed with R 3.0.2 (R Core Team 2013) for WINDOWS.

RESULTS

Effect of species identity and species richness

The composition of litter played an important role in the decomposition process. The decomposition rate of litter of *D. oldhamii* was much higher than that of litter originating from any other investigated species, with the order being *D. oldhamii* > *I. polycarpa* > *C. camphora* > *A. fortunei* (Fig. 1). The litter mixture containing litter from *D. oldhamii* and *I. polycarpa* showed an ~37.79% higher mass loss rate than litter without the contribution of these two species, probably due to the higher decomposition rates of litter of these species.

The decomposition rates differed significantly among treatments with different litter composition in terms of the species and/or seed family identity that produced the litter, even if the diversity remained the same. The mixture of litter from two species, *A. fortunei* and *C. camphora*, showed a lower mass loss rate than the mixture of litter from all the four species. In contrast, the mixture of litter from the other two species, *D. oldhamii* and *I. polycarpa*, showed a higher mass loss rate than the litter mixture of all the four species (Fig. 2a and 2b).

Genetic diversity effect

The decomposition rate ranged from 1.135 to 1.269 (Table 2) and increased linearly with the seed family richness when disregarding the species identity and excluding the only outlier that corresponded to the four species and mono-family combination ($R^2 = 0.5829$, $P < 0.05$, Fig. 3). In fact, the genetic diversity in this case was related to species diversity. In the two-species litter mixture, genetic diversity showed no significant effect on mass loss rate, except when the litter mixture was composed of litter from *C. camphora* and *D. oldhamii*, whose mass loss rate decreased with increasing genetic diversity (Fig. 4a). In the four species litter mixture, the mass loss rate increased with increasing genetic diversity of each species (Fig. 4b).

Null interaction of species and genetic diversity

Litter mass loss was affected by four factors: (i) species diversity; (ii) genetic diversity; (iii) litter composition and (iv) harvest time. However, no interactive effect of species diversity and genetic diversity on mass loss was detected (Table 3). Indeed, no difference was found between the observed mass loss and the expected mass loss, suggesting that only an additive effect occurred in the mixed treatments (Fig. 5).

Initial litter chemistry

The total N, P, C:N and N:P differed across all seed families (Table 4). *D. oldhamii* showed the largest intraspecific differences in total C and total P, whereas *C. camphora* showed the largest intraspecific differences in total N. The litter decomposition rate was found to be unrelated to the initial C, whereas
it was negatively correlated with the initial total N and N:P. However, the regression curves of litter decomposition rate against total P and C:N displayed quadratic parabolas opening upward and downward, respectively, with the inflection points occurring when total P and C:N were ~0.80 mg g⁻¹ and 48.02, respectively (Fig. 6).

**Figure 1:** the mass loss of litter of single seed families and of a conspecific seed family litter mixture of *A. fortunei* (A), *I. polycarpa* (I), *C. camphora* (C) and *D. oldhamii* (D). A single seed family is denoted as the initial letter of species name followed by a hyphen and an Arabic number (assigned when planted in the nursery), and the mixture of conspecific seed families is denoted as the initial letter of the species name followed directly by an Arabic number indicating the number of seed families involved. The bars with the same letter in a same panel are not significantly different at \( P = 0.05 \).

**Figure 2:** the relationship between species composition and mass loss. The letters A, C, I and D on the horizontal axes stand for the species *A. fortunei*, *I. polycarpa*, *C. camphora* and *D. oldhamii*, respectively. The mass loss rates of leaf litter from *A. fortunei*, *C. camphora* and both (a) and *I. polycarpa*, *D. oldhamii* and both were compared to that of leaf litter mixture of all the four species. The Arabic numbers represent the numbers of seed families incorporated. The bars with the same letter in a same panel are not significantly different at \( P = 0.05 \).
Since litter decomposition rates differ across different species, the species composition of a litter mixture is an important factor influencing litter decomposition. Such additive effects also hold for seed family litter mixtures. When disregarding the species identity, the decomposition rate of a litter mixture increased with an increasing number of constituent seed families. In particular, the litter mixture of all the four species showed a trend of increasing decomposition rate with the increasing number of seed families that each species contained. A null interaction of species and genetic diversity was detected, and only an additive effect occurred in the litter mixture. Litter decomposition was found to be negatively affected by initial total N and N:P.

In the treatments where each species contains four seed families, the mass loss rate of the litter mixture of the four studied species was higher than the mean of the mass loss rates of the litter of the individual four species (Table 2). The distinct variation in decomposition rate among the four studied species is a prerequisite for mixing effects (Bruder et al. 2014; Gessner et al. 2010; Lecerf et al. 2011; Tardif et al. 2014). This is consistent with most of the previous studies showing that species diversity has positive effects on litter decomposition (Barantal et al. 2011; Liu et al. 2009; Quested et al. 2002). Decomposition rates may be increased due to nutrient transfer from high quality to poor quality litter in litter mixture experiments (Hoorens et al. 2010; Schimel and Häggenschwiler 2007). Bonanomi et al. (2014) conducted a decomposition experiment using Hedera helix and Quercus ilex leaf litter, cellulose strips and woody sticks as the materials, and reported an increase in N content of N-poor materials in all treatments wherever they were paired with N-rich litters, coupled with a decrease of N content in the latter material. Moreover, mixed leaves with differing quality can change the chemical environment, and leaf structure can alter total litter

DISCUSSION

<table>
<thead>
<tr>
<th>Species diversity</th>
<th>Genetic diversity</th>
<th>Model</th>
<th>Correlation coefficient</th>
<th>Decomposition rate (a⁻¹)</th>
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<tr>
<td>Mono-species</td>
<td>Mono-family</td>
<td>$y = e^{-1.232t}$</td>
<td>0.4685**</td>
<td>1.232</td>
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<td></td>
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<td>0.5201**</td>
<td>1.224</td>
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<tr>
<td>Two species</td>
<td>Mono-family</td>
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<tr>
<td></td>
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<tr>
<td></td>
<td>Four-families</td>
<td>$y = e^{-1.257t}$</td>
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<td>1.255</td>
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<tr>
<td>Four species</td>
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<td>0.6710**</td>
<td>1.269</td>
</tr>
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</table>

**0.001 ≤ P ≤ 0.01.

**Figure 3:** The relationship between genotypic richness and decomposition rate. Linear regression analysis was used with the outlying open circle excluded.

**Figure 4:** The relationship between genetic diversity (GD1, GD2 and GD4 means 1, 2 and 4 seed families were involved for each species) and mass loss in a two-species litter mixture treatment (a) and in a four species litter mixture treatment (b). The letters A, C, I and D on the horizontal axes represent the species A. fortunei, I. polycarpa, C. camphora and D. oldhamii, respectively. The asterisk in panel (a) indicate significant difference between the three genetic diversity levels of the same species combination. The bars with the same lowercase letters in panel (b) are not significantly different at $P = 0.05$. 

Table 2: The decomposition rates of all treatments as derived by curves generated by Olson's negative exponential model
Table 3: results of repeated-measure ANOVAs for mass loss rate from the start to the end

<table>
<thead>
<tr>
<th></th>
<th>d.f.</th>
<th>F value</th>
<th>P value</th>
</tr>
</thead>
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<td>25.66</td>
<td>***</td>
</tr>
<tr>
<td>Species diversity (SD)</td>
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<td>27.33</td>
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<td>Litter composition (com)</td>
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<td>***</td>
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<td>Harvest time (time)</td>
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<td>142.30</td>
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<tr>
<td>SD × time</td>
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<td>0.67</td>
<td>0.613</td>
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<tr>
<td>GD × time</td>
<td>4</td>
<td>0.65</td>
<td>0.627</td>
</tr>
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</table>

***P ≤ 0.001.

**Figure 5:** observed mass loss of litter mixtures as a function of expected mass loss across all litter mixture treatments. Each point represents an individual container and the dashed line defines identical observed and expected mass loss values. Paired t-test was used to test the difference between observed mass loss and expected mass loss (t = 0.0525, P = 0.9581).

...surface where decomposition occurs in the field (Hector et al. 2000). Pérez Suárez et al. (2012) observed that facilitative and inhibitory mechanisms for mass loss in *Quercus potosina* and *Pinus cembroides* were controlled by the interaction between physicochemical litter characteristics and rainfall in a temperate semiarid forest.

Our study found a significantly positive relationship between litter decomposition and genetic diversity when excluding the only outlier that corresponded to four species and a mono-family combination. At present, we cannot account for this outlier. In fact, the effect of genetic diversity was not separated from that of species diversity in this case. However, such a positive effect of genetic diversity on litter decomposition was corroborated by Miao (2009), who found that the leaf litter decomposition rate of *Solidago canadensis* increased with genotypic richness, and that the mass residue of a single genotype treatment was 29.65% higher than that of the mixture of 12 genotypes. A relatively weak effect of genetic diversity on the decomposition processes was also found in an experiment using leaf litter of *Populus tremuloides* (Madritch et al. 2006). However, to clearly show the effects of genetic diversity on the litter decomposition without confounding effects of species diversity, these previous experiments contained only single species with different numbers of genotypes. In fact, the effect of the composition of mixed litter in terms of species and/or seed family identity might be more important than diversity itself for litter decomposition (Wardle et al. 2003).

To identify the effects of species compositions on litter decomposition, we compared the mass loss rate of single species litter with mixed litter treatments (Fig. 2). We found that species composition played an important role, and that the effect of species composition in mixture experiments should not be neglected (Table 3). In recent years, an increasing number of studies have investigated species composition or species component effects on the decomposition of mixed litter (Maisto et al. 2011; Quested et al. 2002; Zhang et al. 2014). Zhang et al. (2013) reported that the litter mixture of *Leymus chinensis* and *Stipa baicalensis* decomposed much faster than the litter mixture of *Leymus chinensis* and *Melisitus ruthenica*, and almost all studied species showed higher litter decomposition rates when mixed with other species than litter of single species. Species and/or genetic composition of a litter mixture likely determine the litter decomposition rate as litter of different species and/or genetic origin differ in physical, chemical and biological characteristics (Gartner and Cardon 2004).

We did not observe a significant interactive effect between species diversity and genetic diversity (Table 3, Fig. 5). Although several studies have examined the relationship between decomposition and either species diversity (Barantal et al. 2015; Gessner et al. 2010; Hobbie et al. 2006; Lecert et al. 2011) or genetic diversity (Madritch et al. 2006; Wang et al. 2014), the present study investigated the independent and interactive effects of both diversity components on decomposition. We found no significant effect of the interaction of species diversity and genetic diversity on decomposition, suggesting that these two diversity components affect litter decomposition independently.

The initial litter stoichiometry is also the main controlling factor besides environmental factors affecting decomposition. The initial C, N and P contents are very important for litter decomposition (Hättenschwiler and Jorgensen 2010; Talbot and Treseder 2012). The C:N ratio (especially lignin:nitrogen ratio) is regarded as the predictor of the decomposition process. The N and P composition of a given species tends to vary significantly with the available N and P in their environments, and N:P is used as a tool to assess whether the availability of N or P is more limiting for the carbon cycling process in ecosystems (Cornelissen et al. 2003; Gusewell and Gessner 2009;
Koerselman and Meuleman (1996). Smith and Bradford (2003) found that when the litter of the same species but with different initial nitrogen concentrations were mixed, negative, non-additive effects on decomposition were generally observed; however, increasing litter quality richness from two to four mixtures had no significant, non-additive effect on decomposition.
Generally, leaf litter with rich nutrition (low lignin and high N) decomposes faster than litter with poor nutrition (Wardle et al. 1997). Contrary to what would be predicted, a significantly negative relationship between the litter decomposition rate and N content or N:P ratio was observed in the present study. It should be noted that the litter N:P values of most of the microcosms were >16; therefore, litter decomposition was most likely limited by P and not by N (Koerselman and Meuleman 1996). Other leaf characteristics, such as secondary compounds in plant litter and litter physical traits, may affect the decomposition in combination with the litter chemical traits (see Aerts et al. 2012). A. fortunei is a species with rich nutrition (high N and P). Due to the morphological characteristics of A. fortunei litter, the decomposition rate of this litter was lowest among all the four examined species in our study. Dried leaves of A. fortunei take up a curled shape, thereby reducing the contact between leaves and the soil surface, and consequently retarding decomposition. The mass loss rate was also suppressed by the high N content of the leaf litter, which could reduce the activity of lignin lytic enzymes (Berg and McClaugherty 2003).

In contrast to the negative effect of genetic diversity on tree growth found in the same site (Hahn et al. 2017), we identified a positive effect of genetic diversity on leaf litter decomposition. Such an effect will undoubtedly facilitate the turnover and cycling of carbon and nutrients, which might change soil fertility and the microbial community, thereby modifying plant growth and ecosystem productivity. To some extent, the results of our microcosm experiment may be transferable to natural field conditions, as the temperature and humidity conditions in the microcosms were controlled to represent the averages of the season in the subtropical forest in which our litter was collected. However, it should be emphasized that lignin, cellulose and any other factors potentially influencing decomposition were not measured in our experiment, and we only focused on the effects of litter diversity and composition in terms of species and/or genetic identity, and those of litter stoichiometry. In addition, our experiment did not allow us to predict the effect of litter diversity acting during the more advanced stage of decomposition because of the limited duration. Future studies should focus on the species and/or genetic diversity and composition of litter mixture, as well as the stoichiometry of leaf litter and the transformation of chemical components during the decomposition process. Moreover, to what extent the litter decomposition is affected by the species and/or genetic diversity of the standing plants in the environment should also be further investigated, because the surrounding plants are assumed to modify the microclimate and soil fauna, and these changes will certainly affect litter decomposition (Eichenberg et al. 2017).

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