Influence of evenness on the litter-species richness–decomposition relationship in Mediterranean grasslands

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Abstract

Aims
Human impacts on natural ecosystems induce changes in their functioning through alterations in species richness, composition and evenness of plant communities. Most litter diversity–decomposition processes studies have only manipulated species richness, ignoring the role of evenness. Here, results from a field litterbag experiment are presented to test whether changes in evenness of species distribution in litter mixtures affected the strength of the litter-species richness–decomposition relationship.

Methods
Ten herbaceous species abundant in Mediterranean grassland communities and representative of different genera and functional groups were used. Species richness was directly manipulated to produce litter mixtures of three and six plant species, as well as litter of each individual species used. Each level of species richness was replicated several times such that each repeat had a different species composition. Three- and six-species litter mixtures were also treated to vary in evenness (three levels). Decomposition rate was assessed by percentage dry weight loss over the 90 days of the experiment.

Important Findings
Decomposition rate was positively related to the linear increase in litter-species richness and was affected by the composition of the litter-species mixture. Decomposition rates differed significantly between evenness treatments and moreover, the strength of the positive relationship between litter-species richness and decomposition rate decreased notably in the low-evenness treatment. The effects of evenness on decomposition rate, at different richness levels, were partially explained by the differences in the initial litter mixture's carbon-to-nitrogen ratio within them. This study reveals that short-term decomposition rate is positively affected by both components of Mediterranean grassland litter-species diversity.

Keywords: biodiversity • dominance • ecosystem functioning • old field • plant litter mixture

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INTRODUCTION

The alarming rate of biodiversity loss due to global changes (Sala et al. 2000) is expected to induce changes in ecosystem functioning through alterations in species richness, composition and evenness of plant communities (Chapin et al. 2000). Experimental studies conducted during the last decade have shown that plant species richness positively affects biomass production and other aboveground processes in grasslands, while much less work has been carried out on other key ecosystem processes such as decomposition (see reviews by Balvanera et al. 2006; Hooper et al. 2005; Naeem et al. 2009; Srivastava and Vellend 2005). Decomposition of organic matter is a crucial process for ecosystem functioning, affecting...
nutrient cycling and maintaining primary productivity (Begon et al. 2006).

Studies in which plant litter material of different species had been placed in the same environment found significant differences in their decomposition rates (e.g. Cornelissen 1996). In a recent review, Gartner and Cardon (2004) examining papers published on decomposition in both leaf litter mixtures and litter monocultures of each species reported that decay rates in litter mixtures are often accelerated or decelerated (synergistic or antagonistic responses) in comparison to those expected from single-species treatments, i.e. non-additive effects. Three important points emerged from these studies: (i) grassland ecosystems are covered by only two studies (i.e. Bardgett and Shine 1999 and Hector et al. 2000), (ii) no general relationship between litter-species richness and decomposition processes has been found and (iii) litter-species richness gradients were very narrow, including monocultures of two or three species and litter mixtures that were not frequently treated to vary in their species composition (Hättenschwiler et al. 2005; but see Scherer-Lorenzen 2008).

Community diversity combines species richness and equitability or evenness (Begon et al. 2006). In the majority of plant biodiversity experiments, community diversity has only been treated as species richness (Srivastava and Vellend 2005; but see Wilsey and Polley 2004). Likewise, in litter diversity–soil decomposition studies, species evenness manipulations are also rare (but see Dickson and Wilsey 2009; King et al. 2002). In the context of global changes, the inclusion of evenness in biodiversity–ecosystem functioning studies is important as evenness responds more rapidly to changing environmental conditions derived from human activities than species richness and therefore, it might alter the rate of ecosystem processes before species extinctions occur (Chapin et al. 2000; Hillebrand et al. 2008). For example, the dominance structure of terrestrial plant communities has been found to change by experimental warming (e.g. Walker et al. 2006 for the tundra biome; Klanderud and Totland 2005 for alpine communities), as well as by increasing CO2 levels (e.g. Niklaus et al. 2001 for grassland ecosystems).

The effects of evenness on richness–process rate relationship are ambiguous: positive (e.g. Kirwan et al. 2007), negative (e.g. Roscher et al. 2005) and no effects (e.g. Wilsey and Polley 2004) have been reported (reviewed by Hillebrand et al. 2008). The effects of evenness on process rates may be free from the effects of selection or sampling effect (Polley et al. 2003) (when species with particular traits dominate mixtures; Loreau and Hector 2001) as the relative abundance of species and not their identity changes in mixtures when evenness changes. In contrast, complementarity effect (when niche differentiation or facilitation between species occurs; Loreau and Hector 2001) could be enhanced by evenness (e.g. Kirwan et al. 2007). In the context of litter decomposition, if synergistic interactions such as complementarity or facilitation (e.g. nutrient translocation between species in mixtures) drive decomposition rates, increased evenness will amplify the rate of this process (Hillebrand et al. 2008). Because complementarity effects had been found to increase with increasing richness (e.g. Dimitrakopoulos and Schmid 2004; Loreau and Hector 2001; Spehn et al. 2005), a significant increase in decomposition rate can be anticipated with both richness and evenness increasing due to synergistic interactions.

In this paper, a field experiment was conducted in order to investigate how the evenness of the species used in a multiple-species leaf litter decomposition study influences the relationship between the species richness of the leaf litter used and the decomposition rate. This study directly addresses a question that has not been well investigated in the ecological literature (see Hillebrand et al. 2008 for a review) but which could have far-reaching consequences for modelling decomposition processes in real-world systems. Our study design deviates from the design of other studies carried out either in a regenerating Betula pendula forest in the Scottish Highlands (King et al. 2002) or in a prairie in TX (Dickson and Wilsey 2009) because it simultaneously incorporates in a field experiment multiple treatments that vary in terms of species richness, composition and evenness. Two hypotheses are posed on the effects of litter-species richness and evenness components on the decomposition rates. (i) I hypothesize that leaf litter-species richness will be positively related to decomposition rates. (ii) I hypothesize that species richness and evenness will interact to affect leaf litter decomposition rates with the low-richness low-evenness litterbags to present the lower decomposition rates.

MATERIALS AND METHODS

Experimental design

The litterbag experiment took place in a >15-year-old abandoned arable field in the island of Lesbos, Greece (39° N, 27° E, 30 m above sea level). The grassland supports, on average, 27 ± 1 species per square metre. Floristically, it is dominated by annuals; however, perennials contributed to >80% of its biomass production (Dimitrakopoulos et al. 2005, 2006). The mean annual temperature in the field site is 17.6°C, the warmest month is July (mean 26.5°C) and the coolest month is January (mean 9.6°C). The average annual rainfall is 682 mm. The soil of the field site has a high clay content (71.4% clay, 15.9% silt and 12.7% sand) and an average pH of 7.12 (Dimitrakopoulos et al. 2005, 2006).

Ten grassland species abundant in communities of the study site and representative of 10 genera and 3 functional groups (i.e. grasses, legumes and non-leguminous forbs; Dimitrakopoulos et al. 2006) were used in this experiment (Table 1). Species richness was directly manipulated to produce litter mixtures of three and six plant species, as well as litter of each individual species used (Table 1). Highest richness litter mixture was chosen taking into account the approximate number of species found in freshly produced litter samples in soil surfaces of 10 cm × 10 cm in the grassland communities of the study area. To separate the effects of the particular species from those of richness, each level of species richness was
replicated five times such that each repeat had a different species composition assembled randomly for the species pool (Schmid et al. 2002; Table 1). Three- and six-species litter mixtures were also treated to vary in evenness. Three evenness treatments were used: (i) maximum evenness (all species had equal contribution; Simpson’s evenness index = 1), (ii) intermediate evenness (Simpson’s evenness index = 0.62) and (iii) low evenness (Simpson’s evenness index = 0.41). In intermediate and low evenness treatments, each of the individual species included in a mixture was, in turn, dominant, while the remaining species had equal concentration. Therefore, 7 and 13 litterbags were required for each species combination of three- and six-species litter mixtures, respectively (Table 2). All litter mixtures as well as single-species treatments were replicated twice. A total of 220 litterbags were prepared (Table 2).

Leaf litter samples were collected during the summer of 2005 and then dried (80°C, 24 h), mixed and stored until further use. Litter samples included either freshly produced litter collected from the soil surface (e.g. herbs) or fully senesced standing dead leaves removed from each plant (e.g. graminoids). A litterbag of 10 cm × 10 cm was made, using a nylon mesh with holes of 1.0 mm, and was filled with ~2 g dried plant litter material. In early autumn 2005, litterbags were placed on the soil surface and incorporated into the existing litter layer, trying not to cause large-scale disturbance. Litterbags were randomly allocated within two blocks that covered a total area of 16 m². The environmental parameters (e.g. soil moisture, temperature, pH) were considered homogenous across the area in which the experiment was conducted, due to its small size. Litterbags were collected after 90 days and then washed, dried and weighed.

### Data analysis

The data were analysed with analysis of variance (ANOVA) using multiple regression approaches (Schmid et al. 2002). Decomposition rate was the response variable. For the full data set (including litter monocultures), the following terms were fitted in sequential order: (i) block, (ii) species richness decomposed into linear contrast and deviation from linearity (i.e. the quadratic term of a second-order polynomial for species richness) and (iii) species composition (the 20 different monocultures and mixtures in Table 1) within species richness. ANOVAs of the same structure were also run for maximum-evenness mixtures only producing similar results (data are not presented). The ANOVA model for evenness treatments (only three- and six-species litter mixtures) also included a term for evenness and its interaction with species richness and species composition (see Table 3). The F-ratios for

### Table 1: species compositions of the different litter mixtures and single-species treatments used in the experiment

<table>
<thead>
<tr>
<th>Species mixture</th>
<th>Species richness</th>
<th>Species composition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–10</td>
<td>1</td>
<td>Litter of each individual species: As, Hb, Pc, Fa, Bb, Tr, Hi, Pl, Bt, Ms</td>
</tr>
<tr>
<td>11</td>
<td>3</td>
<td>Pc, Hb, Bb</td>
</tr>
<tr>
<td>12</td>
<td>3</td>
<td>Hi, Ms, As</td>
</tr>
<tr>
<td>13</td>
<td>3</td>
<td>Tr, Pl, Bt</td>
</tr>
<tr>
<td>14</td>
<td>3</td>
<td>Hb, Bb, Fa</td>
</tr>
<tr>
<td>15</td>
<td>3</td>
<td>Bt, Hi, Ms</td>
</tr>
<tr>
<td>16</td>
<td>3</td>
<td>Pc, Hb, Bb, Fa, Tr, Pl</td>
</tr>
<tr>
<td>17</td>
<td>6</td>
<td>Tr, Pl, Bt, Hi, Ms, As</td>
</tr>
<tr>
<td>18</td>
<td>6</td>
<td>Bb, Fa, Tr, Pl, Bt, Hi</td>
</tr>
<tr>
<td>19</td>
<td>6</td>
<td>Pc, Hb, Bb, Fa, Ms, As</td>
</tr>
<tr>
<td>20</td>
<td>6</td>
<td>Pc, Hb, Bt, Hi, Ms, As</td>
</tr>
</tbody>
</table>

Species abbreviations are As = Avena sterilis L. (annual grass); Hb = Hordeum bulbosum L.; Pc = Phalaris coerulea Desf. and Fa = Festuca arundinacea Schreb. ssp. arundinacea (perennial grasses); Bb = Bituminaria bituminosa (L.) Stirton and Tr = Trifolium repens L. (perennial legumes); Hi = Hirschfeldia incana (L.) Lagreze-Fossat (annual non-leguminous forbs); Pl = Plantago lanceolata L., Bt = Bellevalia trifoliata (Ten) Kunth and Ms = Malva sylvestris L. (perennial non-leguminous forbs).

### Table 2: the number of litterbags within each treatment in the study design

<table>
<thead>
<tr>
<th>Species richness</th>
<th>1</th>
<th>3</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species composition</td>
<td>Litter of each individual species: As, Hb, Pc, Fa, Bb, Tr, Hi, Pl, Bt, Ms</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Evenness levels</th>
<th>1–10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
<th>19</th>
<th>20</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum evenness</td>
<td>10</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>20</td>
</tr>
<tr>
<td>Intermediate evenness</td>
<td>n/a</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>45</td>
</tr>
<tr>
<td>Low evenness</td>
<td>n/a</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>45</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>No. of litterbags per block</th>
<th>10</th>
<th>7</th>
<th>7</th>
<th>7</th>
<th>7</th>
<th>13</th>
<th>13</th>
<th>13</th>
<th>13</th>
<th>13</th>
<th>110</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total (two blocks)</td>
<td>20</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>26</td>
<td>26</td>
<td>26</td>
<td>26</td>
<td>220</td>
</tr>
</tbody>
</table>

### Table 3: ANOVA for decomposition rate in the mixture litterbags

<table>
<thead>
<tr>
<th>Line Source</th>
<th>Error df</th>
<th>Type I SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Block</td>
<td>7</td>
<td>1</td>
<td>9.5</td>
<td>9.5</td>
<td>0.192</td>
</tr>
<tr>
<td>2 Species richness</td>
<td>3</td>
<td>1</td>
<td>1501.9</td>
<td>1501.9</td>
<td>8.558</td>
</tr>
<tr>
<td>3 Species composition within species richness</td>
<td>6</td>
<td>8</td>
<td>1404.1</td>
<td>175.5</td>
<td>4.576</td>
</tr>
<tr>
<td>4 Evenness</td>
<td>6</td>
<td>2</td>
<td>1325.0</td>
<td>662.5</td>
<td>17.273</td>
</tr>
<tr>
<td>5 Species richness × evenness</td>
<td>6</td>
<td>2</td>
<td>383.4</td>
<td>191.7</td>
<td>4.998</td>
</tr>
<tr>
<td>6 Evenness × species composition</td>
<td>7</td>
<td>16</td>
<td>613.7</td>
<td>38.4</td>
<td>0.777</td>
</tr>
<tr>
<td>7 Residual</td>
<td>169</td>
<td>8344.5</td>
<td>49.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>199</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

ss = Sum of Squares; MS = Mean Squares. Each line represents a term fitted by the multiple regression approach, allowing mixing of multi-level factors and continuous variables in sequence. Significant values (P < 0.05) are given in bold.
significance tests were calculated as indicated in Table 3 (Schmid et al. 2002). Confounding effects between species identity and richness were avoided dividing mean squares of richness by those of species composition (Schmid et al. 2002). To test if parameters of the initial litter mixture quality affected decomposition patterns, leaf C:N ratio was introduced as a covariate in the ANOVA. Leaf nitrogen concentration (LNC) and leaf carbon concentration (LCC) data were used for each of the 10 species in the experiment (Dimitrakopoulos 2001; PG Dimitrakopoulos, unpublished data) to calculate aggregate values of both traits for each initial litter mixture, based on the formula proposed by Garnier et al. (2004):

\[
\text{LNC}_{\text{agg}} = \sum_{i=1}^{n} p_i \times \text{LNC}_i \quad \text{and} \quad \text{LCC}_{\text{agg}} = \sum_{i=1}^{n} p_i \times \text{LCC}_i,
\]

where \(p_i\) is the relative contribution of the species \(i\) to the total leaf mass of litter mixture, \(n\) is the number of species of litter mixture, and \(\text{LNC}_i\) and \(\text{LCC}_i\) are the leaf nitrogen and carbon concentration, respectively, of the species \(i\) in the initial litter mixture. All analyses were performed using SPSS 16.0 software.

Decomposition rate was assessed by percentage dry weight loss over the duration of the experiment. Expected values of mass remaining (E) for the litter mixtures were calculated based on the mass remaining of their component species in the single-species litters as follows (e.g. Lecerf et al. 2007; Moore and Fairweather 2006):

\[
E = \sum_{i=1}^{S} w_i \times M_i,
\]

where \(w_i\) is the initial weight of the species \(i\) in mixture, \(M_i\) is the residual litter mass in monocolture of the species \(i\), and \(S\) is the total number of species in litter mixture. Deviation between the expected and the observed mass remaining in litter mixtures is calculated using the following formula: \([\text{O} - \text{E}] / \text{E} \times 100\%\) (Loreau 1998). Negative values indicate that mass loss in mixtures is greater than predicted from monoculture values (synergistic effects), and the opposite holds true for positive values (antagonistic effects). Additive effects originate from non-different to zero values.

**RESULTS AND DISCUSSION**

Litter of the different plant species and mixtures decayed ranging from 40% to nearly 80% over the period of the experiment. Rapid decay of litter mass is not uncommon in litterbag experiments (e.g. Moore and Fairweather 2006). Comparable results have been observed in other experiments, using not only leaves but also stems, in terms of both time period and decay rates. For example, Hector et al. (2000) found that the variation in the decomposition of different temperate grassland litter-species mixtures (including both stems and leaves) was very high, ranging from <10% to nearly 80%, for a time period of 85 days approximately. Scherer-Lorenzen (2008) found that a 10-week decomposition rate of above-ground plant litter ranged from 40% to nearly 70%. Radea and Arianoutsou (2004) found that 60% of the dry mass of leguminous leaves and stems (ash free) was decayed after 113 days in a Mediterranean Aleppo pine forest that had been burnt down 18 months before.

Decomposition rate was positively related to the linear increase in litter-species richness (contrast \(F_{(1,17)} = 18.879; P < 0.001\)). These results from Mediterranean grasslands are consistent with the first hypothesis but are in contradiction with the results of the majority of experimental studies conducted in temperate ecosystems in which no significant richness effect was found (e.g. Dickson and Wilsen 2009; Hector et al. 2000; Knops et al. 2001; Moore and Fairweather 2006; Scherer-Lorenzen 2008; Wardle et al. 1997; but see Bardgett and Shine 1999). Likewise, important differences in short- and long-term decomposition rate patterns measured by dry weight loss of cotton strips and birch sticks across a plant diversity gradient between temperate and Mediterranean grassland ecosystems have emerged from the BIODEPTH project: the Greek site presented the strongest richness effects, while weak or no effects were reported from temperate grasslands (Dimitrakopoulos et al. 2006; Scherer-Lorenzen 2008; Speth et al. 2005).

Species composition had significant effects on decomposi-
tion rates \((F_{(17,199)} = 2.676; P = 0.001)\). Results from previous studies conducted in temperate grassland ecosystems suggest that species identity is more important than species richness per se in determining decomposition rate (e.g. Hector et al. 2000; Moore and Fairweather 2006; Scherer-Lorenzen 2008; Wardle et al. 1997). This means that except from the species richness effect, the increase or decrease in decomposition rate of a community is dependent on functional traits of the species added or lost from it (Scherer-Lorenzen 2008).

In three- and six-species litter mixtures, decomposition rates differed significantly between evenness treatments \((P < 0.001;\ Table 3)\) and the linear increase in decomposition with increasing species richness was not similar between evenness treatments (significant ‘species richness \(\times\) evenness’ interaction; Table 3; Fig. 1). The strength of the positive relationship between litter-species richness and decomposition rate decreased notably in the low-evenness treatment (Fig. 1). No significant interaction between species composition and evenness on decomposition rate was detected (Table 2). The C:N ratio of the initial litter mixture had a significant effect on decomposition rate, when it was added as a covariate in the ANOVA \((F_{(1,165)} = 6.31, P = 0.013)\), as in many other studies (e.g. Hättenschwiler et al. 2005; Scherer-Lorenzen 2008). However, the interactive effects between richness and evenness remained significant \((F_{(2,16)} = 4.46, P = 0.029)\). These results support the second hypothesis, confirming that species loss significantly affects the decomposition rate of a community but the magnitude of loss depends on species abundance patterns (Hooper et al. 2005). The effects of evenness on decomposition rate, at different richness levels, were partially explained by the differences in the initial litter mixture’s carbon-to-nitrogen ratio within
them. Consistent with our results, Swan et al. (2009) examining leaf litter decomposition dominated by four forest species in a small stream found significant interaction between richness and evenness in breakdown dynamics. In contrast with these results, King et al. (2002), using a microcosm approach, found no effects of variations in evenness on decomposition processes for leaf litter mixtures composed of tree and dwarf shrub species. However, their work included only one four-species litter mixture in which different evenness treatments were applied and the litter monocultures of its component species. Litterbag experiments conducted by Dickson and Wilsey (2009) in a prairie in TX showed that (i) although greater evenness caused greater decomposition rates, this effect is mainly due to interactions with micro-environmental conditions, (ii) there was no significant interaction between species richness and evenness on decomposition rates, and (iii) species identity and composition influenced decomposition much more than evenness. The influence of evenness on ecosystem functioning has also been examined in grassland plant biomass production studies that have produced inconsistent results (Kirwan et al. 2007; Mulder et al. 2004; Nijs and Roy 2000; Polley et al. 2003; Wilsey and Polley 2004; Wilsey and Potvin 2000). This is because some studies were on annual communities (e.g. Polley et al. 2003), some on perennials (Kirwan et al. 2007; Wilsey and Polley 2004; Wilsey and Potvin 2000), some used legumes (Kirwan et al. 2007) and some did not and some did not vary evenness experimentally (Mulder et al. 2004).

The deviation of the values of mass remaining in the mixture litterbags from the expected ones was negatively correlated with litter-species richness for each evenness treatment (Fig. 2), but the intensity of association was increased from the low-(Pearson correlation: $r = -0.297$, $n = 90$, $P = 0.005$) and the intermediate-evenness distributions ($r = -0.593$; $n = 90$, $P < 0.001$) to the maximum ones ($r = -0.647$, $n = 20$, $P = 0.002$). ANOVA results for the deviation from expected litter mass remaining confirmed that its negative relationship with species richness became steeper with increasing evenness (significant ‘species richness $\times$ evenness’ interaction; $F_{(2,16)} = 3.868$, $P = 0.04$). No significant effects of species composition were detected ($P > 0.05$). These results suggest synergistic litter-richness effects on decomposition, as reported in other studies (e.g. Hector et al. 2000; Moore and Fairweather 2006), that increase with increasing evenness.

These results could be attributed to two possible mechanisms. These synergistic litter-mixing effects could be caused by nutrient translocations between species (Hättenschwiler et al. 2005). The combination of high- and low-quality litters in high-diversity litter probably accelerates the decomposition rate of the mixture due to complementary nutrient transfer among litter types (e.g. Wardle et al. 1997), although results from some experiments do not support this hypothesis (e.g. Hoorens et al. 2003; Wardle et al. 2006). Second, litter-mixing effects may be increased because of improvement of micro-environmental conditions for soil fauna, i.e. increasing structural heterogeneity of litter (Hättenschwiler et al. 2005; Moore and Fairweather 2006).

In conclusion, this study revealed that short-term decomposition rate is positively affected by both components of litter-species diversity in Mediterranean grasslands. Given that

![Figure 1](https://academic.oup.com/jpe/article-abstract/3/2/71/906849/7415868)
Figure 2: Percent deviation from expected litter mass remaining in the mixtures \([100 \times (\text{observed} - \text{expected})/\text{expected}]\) as a function of litter-species richness for the maximum-evenness (a), intermediate-evenness (b) and low-evenness (c) treatment.
anthropogenic impacts on natural ecosystems induce significant changes on species abundance patterns in the direction of higher dominance, biodiversity–functioning studies have to incorporate evenness together with richness for diversity measurements (Dangles and Malmqvist 2004; Stirling and Wilsey 2001; Swan et al. 2009; Wardle 2002; Wilsey and Potvin 2000).

Future research should focus on the relative importance of (i) litter diversity components on longer-term decomposition processes, (ii) species-specific responses within the litter mixtures of varying diversities for decomposition processes and (iii) litter diversity components on richness and abundance of soil organisms.

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