Home-field advantages of litter decomposition increase with increasing N deposition rates: a litter and soil perspective

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Summary

1. Differences in litter quality and in soil microbial community composition can influence the litter decomposition and ‘home-field advantage’ (HFA). However, our knowledge about the relative role of litter and soil characteristics on litter decomposition and HFA effects is still limited, especially under long-term N deposition.

2. We collected soil and two types of litter (monospecific and mixed species litter) from five replicate plots from a long-term N deposition field experiment with seven N addition treatments (0, 2, 5, 10, 15, 20, 50 g N m\textsuperscript{-2} year\textsuperscript{-1}). We examined the effects of N addition on litter quality and soil characteristics. We then carried out a three-pronged microcosm decomposition experiment with (i) litter from different N addition treatments decomposed on a standard field soil; (ii) standard litter decomposed on soils from the different N addition treatments; and (iii) litter decomposed on soil from the same N addition treatment plot.

3. Decomposition of litter on standard soil was influenced strongly by the N addition treatment, but did not consistently decrease or increase with increasing N addition rates. Instead, decomposition of standard litter on soils collected from different N addition treatments decreased with increasing rates of N addition. Decomposition of litter on soil collected from the same plot increased with increasing N addition rates. Soil characteristics explained more of the variation in litter decomposition than litter characteristics.

4. There was a clear HFA effect for litter decomposition, both from a litter and from a soil perspective. HFA effects increased when the dissimilarity in litter quality (N content and C : N ratio) increase among the different N addition treatments and the soil effect was strongest at high N addition rates.

5. N addition influenced litter decomposition by changing both litter and soil characteristics. Importantly, N addition decreased the capability of soils to decompose litter and it increased the HFA effect indicating that soils decomposed local litter better than other litter, due to specialization in soil communities. Nitrogen deposition is an important threat to ecosystems worldwide and our study emphasizes that ecosystem functions such as decomposition can be greatly influenced by these global changes.

Key-words: decomposition, home-field advantage, litter quality, mixed litter, N addition, soil community

Introduction

In terrestrial ecosystems, the majority of the above-ground primary production enters the soil system as plant litter (Bardgett & Wardle 2010). The breakdown of plant residue will depend not only on the quality or community composition of the litter, but also on physiochemical conditions of the soil and the composition, abundance and activity of biota in the soil that breakdown the litter.
(Cadisch & Giller 1997; Hättenschwiler, Tiunov & Scheu 2005). Among the factors that determine the decomposition rates, the concentrations of nitrogen (N) and phosphorus (P) of the litter as well as the composition of structural carbohydrates are relatively important (Melillo, Aber & Muratore 1982; Cadisch & Giller 1997). Faster decomposition rates are often correlated with high initial N concentrations and less cellulose material (Cadisch & Giller 1997). Differences in the chemical composition of the litter can also influence the activity and composition of the soil decomposer community (van der Putten et al. 2009). In addition, the soil community can also be influenced directly by changes in soil physiochemical characteristics (Keiser et al. 2011). Hence, litter quality, soil abiotic factors and the composition of the decomposer community all interact to influence the decomposition rates.

A rapidly increasing number of studies have shown that litter decomposes faster in its habitat of origin than in other habitats, indicating that home soil communities are adapted to decompose local litter (Ayres et al. 2009). This is called the ‘home-field advantage’ (HFA) effect (Freschet, Aerts & Cornelissen 2012). However, HFA effects may vary in magnitude and direction (Wang, Zhong & He 2013; Veen, Sundqvist & Wardle 2015b; Veen et al. 2015a). For example, Perez et al. (2013) found different HFA effects along a plant successional gradient from grassland to forests. The functional breadth hypothesis suggests that a soil community from a nutrient-poor environment has a wider functional capacity and can degrade a broader range of organic compounds than that from a rich environment due to different proportions of specialists in the decomposer community (Keiser et al. 2011; Fanin, Fromin & Bertrand 2016). This specialization under nutrient enrichments implies that HFA effects will be stronger in nutrient-rich than nutrient-poor systems. A meta-analysis of litter transplant experiments suggests that HFA may also increase with increasing dissimilarity in litter quality (N content and C : N ratio) in the home vs. away contrast (Veen et al. 2015a). Thus, differences in litter quality or in the composition of soil organisms can influence the HFA effects (Milcu & Manning 2011; Keiser et al. 2014). However, our knowledge about the relative role of litter quality and the soil community on litter decomposition and HFA effects is still limited (Berg & McClaugherty 2003).

Due to fossil fuel combustion and agricultural practices, atmospheric deposition of N has increased over the past decades, and is projected to increase further in coming years (Galloway et al. 2008). The growth of most plants is N limited, and N addition via atmospheric deposition can result in increases in the concentration of N and P contents in the foliage of the plant, and hence improve the quality of litter that enters the soil (Elser et al. 2007; Liu et al. 2016). Furthermore, N fertilization often leads to changes in the composition of plant communities, as fast growing plants generally benefit more from increased soil fertility than slow growing ones (Stevens et al. 2004; Pierik et al. 2011). Hence, N deposition may also influence the quality of litter via changes in the composition of plant species and hence influence the decomposition processes. Nitrogen deposition can also influence soil biological communities involved in decomposition processes, either directly through influencing soil microbial biomass (Treseder 2008), microbial carbon use efficiency (Manzoni et al. 2012; Spohn 2015), microbial community composition (Fierer et al. 2012; Ramirez, Craine & Fierer 2012; Leff et al. 2015), and changes in extracellular enzymes (Alster et al. 2013) or indirectly through the stimulation of litter inputs to the soil (Bardgett & Wardle 2010). Previous studies have reported both positive and negative N deposition effects on litter decay rates (Berg & Matzner 1997; Knorr, Frey & Curtis 2005; Hobbie et al. 2012; Riggs et al. 2015), but few studies have compared litter decomposition and HFA effects from a soil and litter quality perspective under conditions of long-term N deposition (Manning et al. 2006).

We collected soil and litter from a field experiment with seven N addition treatments (0, 2, 5, 10, 15, 20, 50 g N m\(^{-2}\) year\(^{-1}\)) in semi-arid grassland in northern China. Using those soil and litter samples, we set-up a three-pronged microcosm decomposition experiment in a controlled laboratory environment. Specifically, we tested the following hypotheses. (i) N addition will positively influence litter quality and accelerate decomposition. (ii) N addition will negatively influence the decomposition capacity of the soil (cs functional breadth hypothesis). (iii) Litter will decompose faster in its home soil than in a standard soil, and local litter will decompose faster than standard litter in home soil (HFA effect). Finally, as we predict that soil decomposer communities from a N-rich environment will degrade labile litters faster than recalcitrant litters, we hypothesize that (iv) N addition will increase the HFA effect.

**Materials and methods**

**LITTER AND SOIL COLLECTION**

Soil and litter were collected from a long-term N addition experiment located at a temperate steppe near the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 116°14'E, 43°13'N). The field experiment was fenced and has been maintained since September 2008. Mean annual temperature in the study area is 0–9 °C, with mean monthly temperatures ranging from –21.4 °C (January) to 19.7 °C (July). The mean annual precipitation is 355.3 mm, about 60–80% occurs in the growing season from May to August. The plant community in the area is dominated by the grasses *Leymus chinensis* (Trin.) Tzvel. and *Stipa grandis* P. Smirn (Poaceae), which accounted for more than 60% of the total above-ground biomass. The soil is a Haplic Calcisol according to the FAO classification system and ambient total N deposition is less than 1.5 g N m\(^{-2}\) year\(^{-1}\) in this area.

The details of the experimental design of the field experiment have been described elsewhere (Zhang et al. 2014). Briefly, there were nine levels of N addition (0, 1, 2, 3, 5, 10, 15, 20, 50 g N m\(^{-2}\) year\(^{-1}\)) applied at two frequencies: either 2 times per year or monthly. For the current study, we selected seven N addition levels (0, 2, 5, 10, 15, 20, 50 g N m\(^{-2}\) year\(^{-1}\)) applied at
low frequency (2 times per year). Hereafter, the N addition treatments will be denoted as N₀, N₂, N₄, N₆, N₁₀, N₁₅, N₂₀, and N₅₀. Nitrogen was applied as purified ammonium nitrate (NH₄NO₃ >99%) every year. The treatments mirrored the seasonal pattern of natural N deposition: in June, the NH₄NO₃ was mixed with purified water (all treatments received 9.0 L water; the N₀ treatment received only water) and sprinkled evenly using a sprayer to each plot to simulate wet deposition. In November, NH₄NO₃ was mixed with clean sand (0.5 kg sand per plot) and spread uniformly by hand to simulate dry deposition. Each plot received the same amount of water and sand. The experiment was set up as a randomized block design with 10 blocks of 45 × 70 m each. Each plot was 8 × 8 m in size and the plots were separated by 1 m walkways. For the current experiment, we used plots belonging to five randomly selected blocks (7 treatments × 5 blocks = 35 plots).

At the end of September 2014, when the majority of plants in all plots had senesced, we collected soil and litter from each of the 35 plots. Two types of litter were collected, mixed species litter, hereafter called ‘mixed litter’ and ‘monospecific litter’. The grass L. chinensis was selected as the monospecific litter. Above-ground plant biomass of this species was collected from plants growing throughout the plot ensuring that only senesced plant material was collected. Mixed litter was collected by cutting three 15 × 15 cm quadrats at 2 cm above soil level placed randomly in the plot. The quadrats were at least 50 cm apart and the three samples from each plot were combined. To collect soil, after removal of the surficial litter, three 10 × 10 × 10 cm soil blocks (50 cm apart) were excavated at the centre of each plot using a spade and combined to make one sample per plot. ‘Standard’ litter and soil were collected from an untreated area within the fence and outside the plots using the same methods as described earlier. All litter and soil samples were transported to the laboratory within 3 days and outside temperatures during transport were around 10 °C.

In the laboratory, the litter samples were oven-dried at 60 °C to constant weight (~48 h) and then cut into pieces of 1 cm to maximize consistency. From each litter sample, a subsample was oven-dried at 40 °C for 48 h and used for chemical analysis (see below). The soil samples were passed through a 5-mm sieve to remove stones and roots and then stored in a cold place for 1 week before starting the decomposition experiment. Subsamples of soil were kept at -4 °C for 2 weeks before further analysis. Both the ‘standard’ litter and soil material collected from the area outside of the plots were homogenized thoroughly. The general characteristics of standard litter and soil are given in Table 1.

DECOMPOSITION EXPERIMENTS

To determine how N addition influences litter decomposition via its effects on litter quality and soil characteristics, we set up a three-pronged microcosm decomposition experiment. The three experiments ran simultaneously and the units from each experiment were randomly positioned within the laboratory. Hence, the design can be considered as one experiment. In part I, the two types of litter from each of the seven N addition treatments were decomposed in the standard soil. In part II, standard litter was decomposed in the soils from the seven N addition treatments. This design allowed us to compare the N addition effects on decomposition via litter and via the soil. In part III, litter from each N addition plot was decomposed in the soil from the same treatment plot. This enabled us to compare the contribution of litter and soil characteristic to decomposition. By comparing either part I or part II with part III, the HFA effect could be analysed from a litter and soil perspective respectively.

The decomposition experiments were carried out with litterbags placed in microcosms. Plastic cups (6 cm diameter, 5 cm height) were filled with 100 g of soil (fresh weight). Soil water content was determined by oven-drying subsamples at 105 °C for 24 h and soils were adjusted to 20% soil moisture with distilled water. All microcosms were kept in a laboratory with consistent humidity and temperature conditions (10 °C at night and 20 °C during daytime). Ten days later, one stitched nylon litterbag (10 cm diameter, 0.1 mm mesh) containing 1 g of litter was placed on the surface of the soil. Litter was placed in the centre of the litterbag and each litterbag was stitched on the cup to ensure contact with the soil surface (6 cm diameter). Each microcosm was then covered with non-transparent perforated plastic film to reduce light availability and water loss. There were 280 microcosms for each of the three parts of the experiment (7 N treatments × 5 replicate blocks × 2 litter types × 4 time points). After 30, 60, 90 and 120 days, one microcosm was harvested for each block and treatment (70 per experiment). During the experiment, soil moisture levels were controlled by weighing each microcosm every 3 days and adding the necessary amount of distilled water on the top of the litter. The litterbags were oven-dried at 60 °C for 48 h. Litter was then removed from the litterbags, and each sample was gently sieved through a 1-mm mesh to dislodge any adhering soil particles. The litter was then weighed and the remaining dry mass was determined.

CHEMICAL ANALYSES OF SOIL AND LITTER SAMPLES

Chemical analyses were performed on subsamples of litter and soil collected from each of the 35 plots of the field experiment, and of the standard litter and soil (three replicates). Total carbon (TC) and total nitrogen (TN) contents in each soil sample (air-dried and sieved through a 0.15-mm sieve) were determined using a TruSpec CN Elemental Analyzer (Leco Corporation, St Joseph, MI, USA). Total phosphorus (TP) content in the soil was measured by persulfate oxidation followed by colorimetric analysis (Olsen & Sommer 1982). To determine soil dissolved organic carbon (DOC), 10 g fresh soil sample (sieved through a 2-mm sieve) was extracted with 20 mL deionized water and then analysed using Multi N/C 3100 Analyzer (Analytik Jena company, Jena, Germany). Soil pH was measured in 1 : 2.5 soil : water suspension with a pH meter (Thermo Fisher Scientific Inc., Waltham, MA, USA). Soil water content was determined by oven-drying.

Table 1. General properties of standard litter (mixed and monospecific) and standard soil

<table>
<thead>
<tr>
<th>Litter</th>
<th>Mixed</th>
<th>Monospecific</th>
<th>Soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>C (mg g⁻¹)</td>
<td>576.6 ± 10.0</td>
<td>534.7 ± 8.6</td>
<td>C (mg g⁻¹)</td>
</tr>
<tr>
<td>N (mg g⁻¹)</td>
<td>10.65 ± 0.27</td>
<td>11.74 ± 0.57</td>
<td>N (mg g⁻¹)</td>
</tr>
<tr>
<td>P (mg g⁻¹)</td>
<td>1.02 ± 0.04</td>
<td>1.09 ± 0.10</td>
<td>P (mg g⁻¹)</td>
</tr>
<tr>
<td>Cellulose (mg g⁻¹)</td>
<td>296.4 ± 4.1</td>
<td>267.0 ± 0.6</td>
<td>DOC (mg kg⁻¹)</td>
</tr>
<tr>
<td>Hemicellulose (mg g⁻¹)</td>
<td>251.9 ± 2.3</td>
<td>288.4 ± 3.1</td>
<td>MBC (mg kg⁻¹)</td>
</tr>
<tr>
<td>Lignin (mg g⁻¹)</td>
<td>196.7 ± 2.6</td>
<td>177.3 ± 6.2</td>
<td>pH</td>
</tr>
</tbody>
</table>

Data are mean ± SE.
subsamples at 105 °C for 24 h. The microbial biomass carbon (MBC) was extracted using a chloroforume fumigation extraction method (Brookes et al. 1985) and then analysed by TruSpec CN Elemental Analyzer (Leco Corporation).

Dried litter samples were ground and sieved through a 0-20 mm mesh for chemical analyses. TC in litter was measured by dry combustion of microsamples using an elemental analyser (Jena Corporation). TN in litter was analysed using the modified Kjeldal method (ISO 1995). TP in litter was measured by persulphate oxidation followed by colorimetric analysis. Cellulose, hemicellulose and lignin content in the litter were measured using the National Renewable Energy Laboratory procedure (Sluiter et al. 1985) and then analysed by TruSpec CN Elemental Analyzer (Agilent Technologies, Santa Clara, CA, USA). Two fractionate forms of lignin, acid-soluble material and acid-insoluble material, were measured by UV-Vis spectroscopy TU-1901 (Purkinje General Instrument, Ltd., Beijing, China) and Muffle furnace (Neytech 3-550; Lab-Pro Incorporated, Sunnyvale, CA, USA). Mass ratios of litter C : N, C : P and N : P were also calculated for further analysis.

C A L C U L A T I O N S A N D S T A T I S T I C A L A N A L Y S I S

To determine the litter decay constant (k-value), we fitted a simple exponential equation:

\[ \frac{M_t}{M_0} = e^{-kt} \]  

where \( M_t \) is the remaining litter mass after time \( t \), and \( M_0 \) is the initial litter mass (Olson 1963). This relationship assumes constant fractional mass loss with time. We calculated \( k \) separately for each replicate of both types of litter (mixed or monospecific; Table S3, Supporting Information).

The three experimental parts were analysed separately with linear mixed effects models (nmlr package, Pinheiro et al. 2016) in R statistical language (version 3.1.2, R Development Core Team) to determine the effects of litter type (mixed or monospecific) and N addition (7 levels, as fixed factors), and their interaction on litter decomposition rates (k-value) and their interaction on litter quality and decomposition rates (k-value) with field plot nested in the block as a random effect. Since significant litter type effects or interaction effects were observed, one-way ANOVA was then used to test the effect of N addition on litter quality (C, N, P contents and ratios, cellulose, hemicellulose and lignin contents) and k-value for each type of litter. Post hoc comparisons were based on a Tukey’s HSD test with adjusted P-values. Data were tested for normality using the Shapiro–Wilk normality test and the assumption for equal variances using a Bartlett test of homogeneity of variances. When necessary, data were natural log transformed to conform to the ANOVA assumption of homogeneity of variance.

We subsequently calculated the HFA effect from a litter perspective (hereafter called ‘litter effect’) and a soil perspective (hereafter called ‘soil effect’). The litter effect is the difference in decomposition rate between a litter from a specific N addition treatment decomposed in its own/home soil and standard litter decomposed in the same soil. The soil effect is the difference in decomposition rate between a litter from a specific N addition treatment decomposed in its own/home soil and the same litter decomposed in control soil. We used the following formulae:

Litter effect = \[ \ln \left( \frac{k_{\text{HFA}_{\text{N}}} \cdot \text{N}}{k_{\text{HFA}_{\text{N}}} \cdot \text{N}} \right) \]  

Soil effect = \[ \ln \left( \frac{k_{\text{HFA}_{\text{N}}} \cdot \text{N}}{k_{\text{HFA}_{\text{N}}} \cdot \text{N}} \right) \]  

where \( N \) indicates the \( x \) nitrogen treatment, \( k_{\text{HFA}_{\text{N}}} \) is the k-value of N\( x \) treatment in part III, \( k_{\text{HFA}_{\text{N}}} \) is the k-value of N\( x \) treatment in part II and \( k_{\text{HFA}_{\text{N}}} \) is the k-value of N\( x \) treatment in part I. Positive litter effects indicate that a specific litter decomposes faster than a standard litter in the home soil, and positive soil effects indicate that a specific litter decomposes faster in the home soil than in standard soil. Differences at \( P < 0.05 \) were considered significant.

We used variance partitioning to estimate the contribution of litter characteristics and soil characteristics on litter decomposition based on the k-values of part III where both litter and soil characteristics varied. Data were analysed using linear constrained multivariate analysis (RDA) in CANOCO Version 4.5 (Plant Research International, Wageningen, the Netherlands) to examine the effects of litter characteristics and soil characteristics on litter decomposition. Litter characteristics included in the analyses were C, N, P contents and ratios, cellulose, hemicellulose and lignin contents. As soil characteristics, we included C, N, P contents and ratios, pH, MBC and DOC. These characteristics were entered as environmental variables in the analyses. k-values were used as response variable. The analyses were run separately for the two types of litter (monospecific or mixed). F-values and P-values were based on a permutation test (499 permutations). We used a split plot design with blocks as whole plots and plots as split plots. Split plots were permuted freely, and whole plots were not permuted.

R E S U L T S

E F F E C T S O F N A D D I T I O N O N L I T T E R Q U A L I T Y A N D S O I L C H E M I S T R Y

Characteristics of the two types of litter varied significantly. The concentrations of total C, cellulose and lignin were higher in mixed litter, whereas total P and total N were higher in monospecific litter (Fig. 1). In both types of litter, the concentration of N and P increased with increasing rates of N addition (Fig. 1b,c). Cellulose and hemicellulose concentrations decreased with increasing N addition rates, but this was particularly so for mixed litter, resulting in significant N addition × litter type interactions (Fig. 1d,e). For monospecific litter, cellulose, hemicellulose and lignin concentrations were highest in the N\( 5 \) treatment (Fig. 1). The ratios of C : N and C : P decreased with increasing N addition rates in both types of litter (Fig. S1). N addition did not affect the ratios of N : P in mixed litter, whereas for monospecific litter, the ratio of N : P was the lowest in the N\( 5 \) treatment (Fig. S1).

There were no significant differences in soil total C, N and P concentrations (0–10 cm layer) among the N treatments (Table 2). The concentration of DOC in the soil increased at the highest levels of N addition, whereas MBC (range 291 to 26 mg g\( ^{-1} \)) and soil pH (range 7.27 to 4.43) decreased sharply with increasing N addition rates (Table 2).

L I T T E R D E C O M P O S I T I O N R A T E S

There were significant N addition effects on decomposition rates for all three parts of the microcosm experiment, whereas the effect of litter type (monospecific or mixed)
was significant only in parts II and III (Fig. 2). Decomposition rates of litter collected from each plot and decomposed in standard soil (part I) varied among N addition treatments, but did not differ among litter origins. The highest $k$-values were obtained for litter collected from plots belonging to the N 10 treatment (Fig. 2a). Decomposition of standard litter on the different soils (part II) was overall higher for monospecific litter and decreased with increasing N addition rates, but this was only significant for mixed litter (Fig. 2b). The same pattern was observed when litter from each N addition treatment was decomposed on its home soil (part III), decomposition rates of litter were higher in monospecific litter and increased with increasing N addition rates, but this was only significant for mixed litter (Fig. 2c).

Across all treatments, the $k$-value of mixed litter from N addition plots on standard soil (part I) was positively correlated with total carbon of the litter, whereas the $k$-value of monospecific litter was negatively correlated with total phosphorus of the litter (Table S1). The $k$-value of standard mixed litter on soil from the N addition plots (part II) was positively correlated with soil pH and MBC and...
negatively correlated with soil TN and DOC (Table S2). There were no significant correlations between decomposition of monospecific litter and soil characteristics.

**HFA TEST: LITTER AND SOIL EFFECTS ON DECOMPOSITION**

For both types of litter, the ‘litter effect’ (based on part II and part III) was overall positive, indicating that local litter decomposed faster than standard litter. The positive ‘litter effect’ increased with increasing N addition rates and this effect was stronger for mixed litter (Fig. 3a). The ‘soil effect’ (based on part I and part III) was also overall positive indicating that local litter decomposed faster in home soils than in standard soil. The positive ‘soil effect’ generally increased with increasing N addition rates (Fig. 3b). The multivariate variance partitioning analysis showed that litter and soil characteristics together explained a large part of decomposition of both litter types. However, the explained variance in mixed litter (69%) was higher than in monospecific litter (50%; Table 3). In both types of litter, soil characteristics explained more of the variation in decomposition than litter characteristics. The ‘pure’ effects (i.e. after removing the effects of other characteristics by including them as covariates) of litter and soil characteristics explained 16-0 and 26-2% of the variance in decomposition of mixed litter, respectively, and 14-3 and 23-6% for monospecific litter (Table 3).

**Discussion**

Our study provides clear evidence for HFA effects. Local litter decomposed faster than standard litter on its home soil, and local litter decomposed faster on home soil than on a standard soil as indicated by the positive ‘litter effects’ and ‘soil effects’. These effects were also true when we analysed monospecific litter. Most studies so far show HFA effects for interspecific litter comparisons. Our study exemplifies that HFA effects are also present in intraspecific litter comparisons. Furthermore, our study shows that N addition greatly influences litter decomposition and increases the HFA effect. We disentangled two mechanisms via which N addition can influence decomposition and HFA effects: via changes in (i) the quality of litter and (ii) the soil characteristics. The results of our study suggest that the effects of N addition on the soil characteristics appear more important for decomposition than the effects on litter quality.

**EFFECT OF N ADDITION ON DECOMPOSITION AND HFA EFFECTS VIA LITTER QUALITY**

After 6 years of N addition, litter characteristics varied considerably between litters collected from different N treatments. Remarkably, not only N but also P concentrations of litter increased with increasing N addition rates and this was true for both types of litter. Nitrogen addition can increase soil N availability (Galloway et al. 2008) and decreases N resorption efficiency (Kobe, Lepczyk & Iyer 2005; Lü et al. 2012). This can result in increased N contents in green leaves. Many studies have reported positive relationships between the rates of N deposition and P concentrations in plant litter (Fujita et al. 2010; Lü et al. 2013). In our experimental field, P is not a limiting factor and this, in combination with observed increased phosphatase activity in previous study carried out at the same site (Lü et al. 2013), may explain why we observed increased P levels in litter with increased N addition.

Decomposition of plant detritus is largely conducted by bacteria and fungi that have relatively high N and P contents, indicative of high requirements for these nutrients (Enriquez, Duarte & Sand-Jensen 1993). Thus, litter with high N and P contents would decompose faster than litter with low nutrient contents because high-quality litter may stimulate the growth of the microbial populations (Moore et al. 1999). In contrast, in our study, we did not detect a significant positive relationship between litter quality (N

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**Table 2. Soil abiotic and biotic parameters for the different N addition levels**

<table>
<thead>
<tr>
<th>Treat</th>
<th>TC (mg g⁻¹)</th>
<th>TN (mg g⁻¹)</th>
<th>TP (mg g⁻¹)</th>
<th>DOC (mg kg⁻¹)</th>
<th>MBC (mg kg⁻¹)</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>N₀</td>
<td>20.3 ± 1.3</td>
<td>2.36 ± 0.14</td>
<td>0.37 ± 0.01</td>
<td>24.4 ± 1.6⁶b</td>
<td>291.5 ± 13.0⁶</td>
<td>7.27 ± 0.13⁶e</td>
</tr>
<tr>
<td>N₂</td>
<td>19.0 ± 0.7</td>
<td>2.14 ± 0.08</td>
<td>0.39 ± 0.02</td>
<td>24.4 ± 4.1⁴b</td>
<td>240.0 ± 18.0⁴e</td>
<td>7.61 ± 0.23⁵</td>
</tr>
<tr>
<td>N₅</td>
<td>20.6 ± 1.1</td>
<td>2.32 ± 0.09</td>
<td>0.38 ± 0.01</td>
<td>17.6 ± 3.7⁷</td>
<td>223.7 ± 16.0⁷e</td>
<td>6.96 ± 0.24⁸</td>
</tr>
<tr>
<td>N₁₀</td>
<td>20.6 ± 0.9</td>
<td>2.32 ± 0.08</td>
<td>0.38 ± 0.03</td>
<td>24.5 ± 2.4⁴b</td>
<td>184.4 ± 14.0⁴d</td>
<td>6.39 ± 0.26⁷</td>
</tr>
<tr>
<td>N₁₅</td>
<td>20.3 ± 0.4</td>
<td>2.34 ± 0.02</td>
<td>0.38 ± 0.03</td>
<td>31.4 ± 1.3⁸</td>
<td>155.6 ± 23.0⁸e</td>
<td>5.93 ± 0.43⁹</td>
</tr>
<tr>
<td>N₂₀</td>
<td>21.2 ± 0.8</td>
<td>2.46 ± 0.08</td>
<td>0.39 ± 0.03</td>
<td>32.9 ± 2.4⁷</td>
<td>96.6 ± 19.0⁷e</td>
<td>5.11 ± 0.23⁹</td>
</tr>
<tr>
<td>N₅₀</td>
<td>19.2 ± 0.9</td>
<td>2.50 ± 0.06</td>
<td>0.38 ± 0.02</td>
<td>53.6 ± 2.8⁸³</td>
<td>26.1 ± 10.0³</td>
<td>4.43 ± 0.07³</td>
</tr>
<tr>
<td>F(6,24)</td>
<td>1.4</td>
<td>2.3</td>
<td>0.5</td>
<td>10.6***</td>
<td>28.9*</td>
<td>29.5***</td>
</tr>
</tbody>
</table>

Data are mean ± SE. Different letters indicate significant differences among N treatments (P < 0.05). F-values from a one-way ANOVA on the effects of nitrogen addition. TC, total carbon; TN, total nitrogen; TP, total phosphorus; DOC, dissolved organic carbon; MBC, microbial biomass carbon. *P < 0.05. ***P < 0.001.
and P contents) and litter decay rate. Instead, when litters collected from different N addition treatments were decomposed in standard soil (part I), there was a positive relationship between litter decay rates and total C-content of mixed litter, and a negative relationship with total P content of monospecific litter. Because of the significantly higher N and P contents in litter, the relatively unchanged C content may increase C limitation and competition in microbial communities (Treseder 2008), and finally, influence the litter decomposition. Hence, our results indicate

![Fig. 2. Effects of nitrogen addition (0, 2, 5, 10, 15, 20, 50 g N m⁻² year⁻¹) and litter type on decay rates of litter collected from the N addition plots and decomposed on standard soil (part I), standard litter decomposed on soil collected from the N addition plots (part II) or litter and soil collected both from the same N addition treatment plot (part III). F- and P-values from a two-way ANOVA on the effects of litter type (T) and nitrogen addition (N) are also presented. Data are shown as mean ± SE. Within each litter type, different letters above bars indicate significant differences at P < 0.05 among N treatments based on a one-way ANOVA. *P < 0.05; **P < 0.01; ***P < 0.001.](image)

and P contents) and litter decay rate. Instead, when litters collected from different N addition treatments were decomposed in standard soil (part I), there was a positive relationship between litter decay rates and total C-content of mixed litter, and a negative relationship with total P content of monospecific litter. Because of the significantly higher N and P contents in litter, the relatively unchanged C content may increase C limitation and competition in microbial communities (Treseder 2008), and finally, influence the litter decomposition. Hence, our results indicate

![Fig. 3. Effects of nitrogen addition (0, 2, 5, 10, 15, 20, 50 g N m⁻² year⁻¹) and litter type on the home-field advantage effect via litter ('litter effect'; a) and via soil ('soil effect'; b). F- and P-values from a two-way ANOVA on the effects of litter type (T) and nitrogen addition (N) are also presented. Data are shown as mean ± SE. Within each litter type, different letters above bars indicate significant differences at P < 0.05 among N treatments based on a one-way ANOVA. **P < 0.01. Asterisks below bars indicate significant differences (P < 0.05) from zero.](image)

and P contents) and litter decay rate. Instead, when litters collected from different N addition treatments were decomposed in standard soil (part I), there was a positive relationship between litter decay rates and total C-content of mixed litter, and a negative relationship with total P content of monospecific litter. Because of the significantly higher N and P contents in litter, the relatively unchanged C content may increase C limitation and competition in microbial communities (Treseder 2008), and finally, influence the litter decomposition. Hence, our results indicate

![Table 3. Results of redundancy analysis of soil and plant characteristics on mixed litter decomposition (k-value in part III) and monospecific litter decomposition (k-value in part III)](image)
that litter carbon could be an important limiting factor influencing litter decomposition.

We found a clear HFA effect from a litter perspective. Locally collected litter decomposed faster in its own soil than standard litter in the same soil. In agreement with our hypothesis, the HFA effect increased with increasing rates of N addition and was strongest at high N addition rates. It is important to note that the standard litter and standard soil were collected from unfertilized plots. As litter quality (N content and C : N ratio) increased with increasing N addition levels, our results are consistent with the dissimilarity hypothesis put forward by Veen et al. (2015a), which suggests that HFA effects increase when the dissimilarity in litter quality increases in the home vs. away contrast. Unfortunately, we did not measure the composition of the plants growing in each plot and hence the species composition in mixed litter. However, another recent study at the same experimental site has shown that N addition decreases plant species richness from around eight species at N0 to around four species at N50 (Zhang et al. 2014). Therefore, for the mixed litter, increased N addition rates most likely changed not only the litter quality but also the species composition of litter. Our results therefore also agree with the hypothesis that HFA effects become larger when the composition of the plant community of the home and away site becomes more dissimilar (Veen et al. 2015a). These significant HFA effects when we analysed litter collected from a single species exemplifies that HFA effects are also present in intraspecific litter comparisons. Several studies have predicted that HFA effects are lower for high-quality litter with more easily degradable compounds than for low-quality litter, since decomposition of low-quality litter required specialized decomposers (Ayres et al. 2009; Milcu & Manning 2011). In contrast, our results show that the HFA effects increase with increasing litter N and P contents. Interestingly, two meta-analyses also found that HFA effects positively correlated with the initial litter quality (N content and C : N ratio) (Wang, Zhong & He 2013; Veen et al. 2015a). Soil decomposer communities from high-quality habitats appear to be adapted to decompose high-quality litter, while decomposer communities from low-quality habitats can decompose a broad range of litters (Fierer, Bradford & Jackson 2007; Strickland et al. 2009).

EFFECT OF N ADDITION ON DECOMPOSITION AND HFA EFFECTS VIA SOIL CHARACTERISTICS

Decomposition of standard litter in soils from different N addition treatments generally declined with increasing levels of N addition. We also observed a significant decrease in MBC and an increase in DOC concentrations along the N addition gradient. Decomposer microbes require N to maintain their growth, so we may expect increased microbial activity and decomposition (Enríquez, Duarte & Sand-Jensen 1993). A meta-analysis of N addition effects on soil microbial communities showed that microbial biomass generally declines on average by 15% under larger N loads and longer durations of N fertilization (Treseder 2008). In our study, we used soil from a long-term field experiment, and our results are consistent with this meta-analysis. We propose that the decreased litter decay rate in soils originating from the highest N addition treatments in our study may be the result of the strong reduction in soil pH, resulting in magnesium or calcium limitation or aluminium toxicity in the microbial community (Wei et al. 2013). There were no differences in C : P and C : N ratios among soils from the different N addition treatments, and DOC levels were increased at high N addition rates. Hence, this suggests that the limiting factor for microbial biomass growth may have shifted from resource availability to soil acidity, with negative consequences on litter decomposition. The differences in soil pH among different N addition treatments are substantial (>2 units). Such a steep pH gradient will also influence other soil properties (Aiciego Pietri & Brookes 2008), which may indirectly influence the litter decomposition.

Locally collected litter decomposed faster in its own soil than in a standard soil. Similar to the litter effect, the soil effect was strongest at high N addition rates. The functional breadth hypothesis suggests that a soil community from a nutrient-rich environment can degrade only a narrow range of organic compounds and is less well able to decompose foreign litters than a soil community from a nutrient-poor environment (Keiser et al. 2011). Evidence is accumulating that plants have species-specific decomposer communities (Bezemier et al. 2010; McGuire & Treseder 2010; Freschet, Aerts & Cornelissen 2012). If these decomposer communities are adapted to decompose local litters (Strickland et al. 2009; Madritch & Lindroth 2011), this, in combination with the decreased capability of soils to decompose litter in part II, may indicate that soils decomposed local litter better than other litter, due to specialization in soil communities under long-term N deposition. The increased HFA effect may suggest that the degree of specialization of the decomposer community increases with increasing N levels (Freschet, Aerts & Cornelissen 2012; Yu et al. 2015). Another very important factor could be the large differences in soil pH among different N treatments. There is strong evidence for changes in soil bacterial diversity and community structure with soil pH gradient (Fierer & Jackson 2006; Shen et al. 2013). Griffiths et al. (2011) showed that soil has different dominant groups of bacteria at threshold pH values of 6.9 and 5.2, which lie within the range in soil pH in this study. Although soil pH may not directly generate HFA effect, those indirect effects from soil pH induced by N addition could have great impact on the HFA effect.

Litter quality and soil characteristics are two main factors that influence litter decomposition (Cadisch & Giller 1997). Our results show that N addition can significantly change both litter quality and soil characteristics, and that both these factors influence litter decomposition and HFA effects. Remarkably, soil characteristics explained more of
the variation in litter decomposition than litter characteristics. This is in contrast with results from a recent study where litters from cropland, forest, plantation and grassland were compared; litter origin was more important in regulating decomposition rates than the origin of the microbial communities (Fanin, Fromin & Bertrand 2016). In our study, all litter and soil samples were collected locally from a single field and this may explain why we found stronger effects of soil than of litter characteristics. Further studies carried out in other systems should examine the generality of this response.

In conclusion, N addition influenced litter decomposition through changing both litter and soil characteristics, and these effects depended on the level of N addition. However, soil characteristics explained more of the variation in litter decomposition than litter characteristics. Our study also clearly showed that local litter decomposed fastest in home soil and that the importance of this HFA effect increased with increasing rates of N addition. Since nitrogen deposition is an important threat to terrestrial ecosystems, our study indicates that global changes can greatly influence ecosystem functions such as decomposition.

Authors’ contributions
Q.L., T.M.B. and X.H. conceived the ideas and designed the experiment; Y.L. and J.Y. collected the data; Y.L., Q.L. and T.M.B. analysed the data; Y.L., Q.L., T.M.B., X.L., X.H. and W.L. led writing of the manuscript. All authors contributed critically to the drafts.

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Data accessibility
All data used in this manuscript are deposited in the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.1783 (Li et al. 2017).

References
N addition increases home-field advantages


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Supporting Information

Details of electronic Supporting Information are provided below.

**Table S1.** Analysis of the correlation between litter decay rate from part I and litter quality.

**Table S2.** Analysis of the correlation between litter decay rate from part II and soil characteristics.

**Table S3.** Results of fitting litterbug decomposition data using single exponential equation.

**Fig. S1.** Effects of nitrogen (N) addition on litter and soil C : N (a, d), C : P (b, e) and N : P ratios (c, f).