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Environmental factors and traits that drive plant litter decomposition do not determine home-field advantage effects

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Summary

- 1. The 'home-field advantage' (HFA) hypothesis predicts that plant litter is decomposed faster than expected underneath the plant from which it originates ('home') than underneath other plants ('away'), because decomposer communities are specialized to break down litter from the plants they associate with. However, empirical evidence shows that the occurrence of HFA is highly variable, and the reasons for this are little understood.
- 2. In our study, we progress our understanding by investigating whether HFA is stronger for more recalcitrant litter types and under colder conditions and how soil properties and plant functional traits affect the magnitude and direction of HFA.
- 3. In subarctic tundra in northern Sweden, we set up a reciprocal transplant litter decomposition experiment along an elevational gradient where three highly contrasting vegetation types (heath, meadow and Salix) occur at all elevations, and where temperature decreases strongly with elevation. In this study, we used a litter bag approach where litters from each elevation \times vegetation type combination were decomposed in all combinations of elevation \times vegetation type. We also measured community-level plant functional traits, such as leaf and litter nutrient content. We determined soil biotic and abiotic properties, such as microbial biomass and soil nutrient content, in soil cores collected for each elevation \times vegetation type combination.
- **4.** We found that mass loss increased with plant and litter nutrient content and with soil temperature. In contrast, the occurrence of HFA was limited in our study system, and its magnitude and direction could not be explained by vegetation type, elevation, plant traits or soil properties, despite these factors serving as powerful drivers of litter mass loss in our study.
- 5. We conclude that although vegetation type and climate are major drivers of litter mass loss, they do not emerge as important determinants of HFA. Therefore, while rapid shifts in plant community composition or temperature due to global change are likely to influence litter mass loss directly by altering environmental conditions, plant trait spectra and litter quality, indirect effects of global change resulting from decoupling of specialist interactions between litter and decomposer communities appear to be of less importance.

Key-words: global change, incubation conditions, litter–decomposer interactions, nutrient cycling, specialization, substrate quality

Introduction

Decomposition of plant litter is a key ecosystem process that drives carbon and nutrient cycling in all ecosystems (Swift, Heal & Anderson 1979), and is primarily controlled by litter quality (Cornwell *et al.* 2008), soil properties

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(Knorr, Frey & Curtis 2005; Liu et al. 2006; Keeler, Hobbie & Kellogg 2009) and macroclimate (Hobbie 1996; Aerts 1997; Trofymow et al. 2002). However, there is increasing recognition that specialized decomposer communities may be important for determining local-scale decomposition processes. As such, there is growing evidence that plant species can sometimes have specific relationships with decomposer communities (Scheu et al. 2003; Bezemer et al. 2010) and that decomposer communities may be specialized to break down litter from the plant with which they are associated (Vivanco & Austin 2008; Strickland et al. 2009b). As a result, litter can decompose faster than expected in the vicinity of the plant from which it originates (i.e. at 'home') than away from that plant, a phenomenon known as the 'home-field advantage (HFA)' effect (Hunt et al. 1988; Gholz et al. 2000; Ayres et al. 2009). However, there is considerable variation in the magnitude and direction of home-field effects, and there are many cases in which HFA does not occur (Freschet, Aerts & Cornelissen 2012; Veen et al. 2015).

In order to better understand HFA and why it occurs strongly in some studies and not others, it is necessary to determine what drives the magnitude and direction of home-field effects. Despite a few recent empirical studies exploring the influence of litter quality on HFA (Milcu & Manning 2011; Freschet, Aerts & Cornelissen 2012; Perez et al. 2013), most aspects regarding how environmental characteristics control home-field effects remain unexplored. However, a recent analyses of 35 published studies on litter transplant experiments suggested that litter quality and macroclimate were not strong predictors of home-field effects, while HFA became stronger when the dissimilarity between litter characteristics and vegetation types increased (Veen et al. 2015). Nevertheless, we have an incomplete understanding as to under which conditions the breakdown of plant litter is favoured by specialized decomposers (Veen et al. 2015). Increased understanding of the drivers of HFA is highly relevant in the context of global change, where altered climate and associated changes in vegetation composition may decouple associations between plants and soil decomposer communities (Berg et al. 2010; Morrien et al. 2010), with consequences for ecosystem processes such as decomposition and nutrient and carbon cycling. Therefore, in this study, we aimed to explore how vegetation type, plant and litter traits, climate and soil properties could potentially impact on the occurrence and strength of HFA.

We explored how vegetation and environmental characteristics affect HFA across a well-established elevational gradient in northern Sweden which ranges from 440 to 900 m (Sundqvist, Giesler & Wardle 2011; Sundqvist *et al.* 2011, 2012; Milbau *et al.* 2013). This system consists of a mosaic of three highly contrasting vegetation types (in terms of plant species composition and plant chemistry) that each occur at all elevations. This makes it possible to study how decomposition processes vary across different vegetation types that have contrasting plant and litter

traits (Sundqvist, Giesler & Wardle 2011). Further, across this gradient, average air temperature during the growing season declines with increasing elevation (Sundqvist *et al.* 2011) and the temperature difference between the highest and lowest elevation is greater than the projected increase in temperature expected to occur in this region within this century (IPCC 2013). This enables the gradient to serve as a powerful tool for studying the influence of climate on decomposition processes (Fukami & Wardle 2005; Sundqvist, Sanders & Wardle 2013). Using the full combination of variation in plant traits and climate that exists across this elevational gradient allows us to determine how different extrinsic drivers influence HFA and thereby help to understand its context dependency.

In this study system, we set up a full-factorial, reciprocal litter transplant experiment where we transplanted litter between the three vegetation types and three elevations. The main aim of our research was to identify how environmental conditions affect the magnitude and occurrence of HFA. We address two overarching questions: (1) how does HFA vary across functionally different vegetation types? And (2) how does HFA vary across an elevational gradient? To answer these questions, we specifically address two hypotheses. Our first hypothesis is that HFA is stronger for vegetation types with recalcitrant litter types than for those with easily degradable litter types, because recalcitrant litter has specific compounds that may need specialist decomposers to break them down (Ayres et al. 2009; Milcu & Manning 2011). Our second hypothesis is that HFA is stronger at lower temperatures (i.e. higher elevations) than at higher temperatures (i.e. lower elevations), because under colder conditions, plant litter may be more recalcitrant (Sundqvist, Giesler & Wardle 2011) meaning that decomposition could be favoured by the presence of specialists (Keiser, Knoepp & Bradford 2013). To further understand the factors that may drive HFA, we also collected detailed measurements on plant and litter traits, soil temperature, and soil biotic and abiotic properties, and attempted to relate variation in these variables to the variation in home-field effects (Veen et al. 2015). Our work will help us to understand to what extent decomposition processes depend on specialized decomposer communities under different environmental conditions and for functionally different vegetation types. It will also advance our knowledge on the ecological consequences of temperature changes that are on a par with those expected to occur in the subarctic over this century (IPCC 2013) and therefore under conditions where plants could become increasingly decoupled from their specialized decomposer communities.

Materials and methods

STUDY SITE

The study was conducted along an elevational gradient on the north-east-facing slope of Mt Suorooaívi (1193 m.a.s.l.), approximately 20 km south-east of Abisko, northern Sweden (68°21′N,

18°49'E) (Sundqvist et al. 2011). For the elevations studied, the mean air temperature during the summer of 2012 (July 6 until August 31) was 10·2 °C at 440 m, 9·2 °C at 690 m and 7·6 °C at 900 m, and during the same period in 2013, it was 11.1 °C at 440 m, 10·3 °C at 690 m and 8·9 °C at 900 m. As global surface temperature is expected to increase by at least 1.2 °C in the coming century (and by at least 2.2 °C in subarctic regions) even under the most optimistic climate change scenarios, the range of temperature across our elevational gradient is relevant to the increase in temperature projected to occur in this region within this century (IPCC 2013). The mean annual precipitation in Abisko is 310 mm (1913-2000; Abisko Scientific Research Station, Abisko, Sweden), with most of the precipitation falling in July (51 mm) and the least in April (12 mm) (Kohler et al. 2006). At the elevational gradient summer precipitation (measured from 26 June to 9 October 2008) ranges between 230 and 290 mm and varies little between elevations (Sundqvist et al. 2014), as was also shown across other elevational gradients in the proximity of our study site (Karlsson, Jonsson & Jansson 2005). The bedrock consists of salic igneous rocks and quartic and phyllitic hard schists (Sundqvist et al. 2011).

Three dominant vegetation types co-occur in a mosaic at all elevations across the gradient: heath-, meadow- and Salix-dominated vegetation. Heath vegetation is dominated by ericaceous dwarf shrubs such as Vaccinium vitis-idaea, V. uliginosum spp. uliginosum and Empetrum hermaphroditum and by Betula nana (Sundqvist et al. 2011). Meadow vegetation and Salix-dominated vegetation are found in shallow depressions, with Salix-dominated vegetation commonly found in more wet locations. Meadow vegetation is dominated by herbaceous species such as Viola biflora, Geranium sylvaticum, Saussurea alpina, Trollius europaeus and Bistorta vivipara and by monocots such as Anthoxanthum odoratum, Deschampsia flexuosa and Carex bigelowii (Sundqvist et al. 2011). The Salix vegetation is dominated by 50- to 100-cm-tall Salix shrubs (which consist of a mixture of several species including Salix glauca, Salix lanata and their hybrids) with an understorey of Gymnocarpium dryopteris, G. sylvaticum and Solidago virgaurea at lower elevations and V. biflora and Equisetum pratense at higher elevations. The tree line is formed by Betula pubescens spp. czerepanovii and is situated at an elevation of approximately 500-600 m.a.s.l. at the study site (Sundqvist et al. 2011); all three vegetation types occur not just above the tree line but also under the tree canopy below the tree line.

EXPERIMENTAL DESIGN

In June 2012, we established five replicate $1 \text{ m} \times 1 \text{ m}$ plots in heath, meadow and Salix vegetation at each of three elevations, that is 440 m (range 423-452 m), 690 m (range 679-707 m) and 900 m (range 890-907 m), resulting in 45 plots in total. These plots were grouped into five blocks, with each block consisting of nine plots, that is, one plot of all possible combinations of elevation and vegetation type. Plots were assigned to blocks based on their elevation within each of the three main elevations; that is, block 1 consisted of the plots that had the highest elevation within each vegetation type within each of the main elevations; block 2 consisted of the plots with the second highest elevation; etc. Within vegetation types within elevations, the median distance between plots was ca. 40 m, and between vegetation types, the median plot distance was ca. 100 m, with a maximum distance of 270 m. Because of the high small-scale spatial heterogeneity in these communities (Björk et al. 2007), this distance is sufficient to ensure adequate independence among plots (Sundqvist et al. 2012). All plots were east or north-east facing, and the mean slope of the plots was 4°.

Between 10 and 13 September 2012, we collected freshly senesced leaf litter of all plant species in each plot, from 5 to 10 randomly placed quadrats of 10 cm × 10 cm each; more quadrats were used in some plots than others to ensure that we had sufficient material from all plots. The litter collected from each plot was bulked and air-dried for at least 48 h until constant weight and cut into 5-mm fragments. For each plot, litter fragments were then homogenized and 0.5 g subsamples were taken to fill each of nine nylon mesh bags (5 cm × 10 cm; mesh size 0.3 mm × 1 mm); these represented community-level subsamples of the litter in the whole plot. A further subsample of litter from each plot was dried at 60 °C for 48 h to determine its moisture content and thus the oven-dry weight of litter in each bag. One of the nine mesh bags sourced from each plot was placed just below the soil surface in undisturbed vegetation in each of the nine plots within its block (with each block consisting of one plot of each elevation × vegetation type combination) on 19 September 2012. This resulted in a full-factorial litter transplant experiment where litter sourced from each vegetation type and elevation was incubated in all vegetation types and elevations. Between 10 and 18 September 2013, we collected the mesh bags and rinsed (0.5 mm sieve), dried until constant weight (60 °C for 48 h) and weighed the litter to determine its litter mass loss during placement in the field.

PLANT AND LITTER TRAITS

In July 2012, we clipped all vegetation in four 10 cm \times 10 cm squares bordering each plot to measure green leaf traits (Table S1, Supporting information). Samples from each plot were bulked and stored in plastic bags at 4 °C for a maximum of 24 h. Harvested vegetation was sorted into species, and stems and leaves were separated. For each species in each sample, we scanned all green leaves (except for all ericaceous dwarf shrubs and B. nana where we used a subsample of ca. 25-50 leaves) to determine total leaf area. In addition, for each species, we determined fresh and dry (60 °C, 48 h) leaf mass. For each species, we used the leaf area and leaf mass measurements to calculate specific leaf area (SLA) as the ratio of leaf area to dry mass, and leaf dry matter content (LDMC) as the ratio of dry to wet leaf mass (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). For each plot, we used these species-level SLA and LDMC measures to calculate whole community-weighted values, by weighting the SLA or LDMC values of each species present by its relative biomass (Garnier et al. 2004). Subsequently, for each plot, we pooled, homogenized and ground all the dried leaves to measure community-level green leaf concentrations of total carbon (C), nitrogen (N), phosphorous (P) and lignin. In addition, we used a subsample of the litter collected in September 2012, which was dried (60 °C, 48 h) and ground, to measure community-level litter C, N, P and lignin concentrations. Carbon and N concentrations were determined by dry combustion using a Leco TruSpec CN Furnace (2004, St. Joseph, MI, USA), P concentration was determined by nitric-perchloric acid digestion (Spark 1996), and lignin concentration was determined by digestion with sulphuric acid. We used plant and litter nutrient concentrations to determine C:N, C:P and N:P ratios.

SOIL PROPERTIES

In July 2012, we collected three to six soil samples in the top 10 cm in each plot with a PVC soil corer (diameter 4.5 cm) to yield a minimum of 0.2 l of soil, for the measurement of soil biotic and abiotic properties (Table S2, Supporting information). Samples were bulked within each plot and stored at 4 °C. Within 48 h after sampling, soil from each plot was sieved to 4 mm, to remove stones and plant roots. Several measurements were performed on subsamples of each soil. Gravimetric soil moisture was determined after drying at 105 °C for 24 h. Soil organic matter (SOM) content was measured by loss-on-ignition in a muffle furnace (550 °C for 4 h). We measured pH in fresh soil (an equivalent of 2·5 g dry soil) using a Mettler Toledo pH meter (Instrument Teknik, Umeå, Sweden) after shaking soil in 40 mL of deionized water (12 h, 150 RPM). Fresh soil (an equivalent of 5 g dry soil) was extracted with 80 mL KCl 1 μ (2 h, 150 RPM) and analysed colorimetrically for concentrations of NH₄⁺, NO₃⁻ and PO₄³⁻ using an Auto Analyzer III (2008, f Analytical; Kontram OmniProcess AB, Solna, Sweden). A soil subsample was dried (60 °C, 72 h) and ground for measurements of total C and N content by dry combustion using a FLASH 2000 Organic Elemental Analyzer (2009; Interscience, Breda, The Netherlands) and P content by nitric-perchloric acid digestion (Spark 1996). We used soil nutrient concentrations to determine C:N, C:P and N:P ratios.

A further subsample of the soil from each plot was freeze-dried and ground, and used for assessing its microbial community using phospholipid fatty acid (PLFA) analysis (Bligh & Dyer 1959; White *et al.* 1979). The PLFA extractions were carried out according to Frostegård, Tunlid & Bååth (1991), and the abundance of PLFAs is expressed in nmol g⁻¹ organic matter (Sundqvist *et al.* 2011). We used i14:0, 14:0, i15:0, a15:0, 15:0, i16:0, 16:1ω9, 16:1ω7c, 16:1ω7t, i17:0, a17:0, 17:1ω8, cy17:0, 17:0, 18:1ω7 and cy19:0 as indicators for bacteria (O'Leary & Wilkinson 1988; Frostegård & Bååth 1996; Zelles 1997) and 18:2ω6 as an indicator for fungi (Frostegård & Bååth 1996; Kaiser *et al.* 2010). We used the PLFA data as proxies for bacterial and fungal biomass and the fungal-to-bacterial ratio (F:B ratio).

On 5 September 2012, we buried one I-button (DS1921G Thermochron; Maxim Integrated, San Jose, CA, USA) in each plot at a depth of 3 cm to measure soil temperature in the uppermost soil layer during the whole litter incubation period. We specified the mean annual soil temperature (measured from 15 September 2012 until 15 September 2013) and the mean summer soil temperature calculated as the mean soil temperature during the months when all plots were snow free (i.e. June to September inclusive). Further, air temperature at each of the three elevations (one logger per elevation, situated in the meadow vegetation type) was measured with a U23 HOBO temperature logger inside a solar radiation shield (Onset, USA) at 15 cm above the soil surface.

DATA ANALYSIS

We used a general linear mixed model (GLMM) to test how source vegetation, source elevation, incubation vegetation and incubation elevation, and all possible interactions among these factors (all as fixed factors) affected litter mass loss, defined as the percentage of mass loss. Block was used as a random factor, with N=5 blocks. Significant interactions between litter source (i.e. the vegetation type or elevation where litter was sourced from) and litter incubation site (i.e. the vegetation type or elevation where litter was incubated) indicate that litter decomposition is different between 'home' and 'away' sites, which may be due to home-field advantage effects; non-significant interactions mean that home-field effects cannot have occurred. When Anova results were significant at P=0.05, differences among means were then explored using Tukey's honestly significant difference (HSD).

To test our hypotheses regarding the drivers of HFA, we further determined the strength and direction of home-field effects on litter mass loss as the percentage of additional decomposition at home (ADH; adapted from Ayres *et al.* (2009) and previously used by e.g. Milcu & Manning (2011) and Giesselmann *et al.* (2011)), calculated using a set of four equations:

$$ADH_i = HDD_i - ADD_i - H,$$
 eqn 1

$$HDD_i = \sum (D_{iI} - D_{jI}), \qquad eqn 2$$

$$ADD_i = \sum (D_{iJ} - D_{jJ}), \qquad eqn 3$$

$$H = \sum HDD_i/(n-1), \qquad eqn 4$$

where ADH_i represents the percentage of additional mass loss of litter type i in its home environment (environment I) relative to away environments; HDD_i represents the difference between the mass loss (D) of litter type i in its home environment I and the mass loss of litter type j (originating from environment J) in environment I; ADD_i represents the difference between the mass loss (D) of species i in environment J and the mass loss of litter type j in environment J; D_{iI} is the mass loss of litter type i in environment I, D_{jI} is the mass loss of litter type i in environment I, D_{iJ} is the mass loss of litter type i in environment I, and D_{jJ} is the mass loss of litter type I in environment I, and I is the mass loss of litter type I in environment I, and I is the sum of all I in the total number of litter types.

To test how vegetation type and elevation affected ADH, community-level plant and litter traits and soil biotic and abiotic properties, we used GLMMs with vegetation type and elevation as fixed factors and block as a random factor. If HFA effects are stronger for recalcitrant litter types (hypothesis 1) and for litter from higher elevations (hypothesis 2), we predict our GLMM will reveal a significant effect of vegetation type and elevation on ADH, respectively. When ANOVA results were significant at P = 0.05, differences among means were explored using Tukey's HSD. We also used both univariate regression and stepwise multiple regression analyses, with mass loss or ADH as response variables, and community-weighted plant and litter traits (see Table S1, Supporting information) and environmental variables (see Table S2, Supporting information) as predictor variables, and with each plot serving as an independent data point so that N = 45. For both simple and multiple regression analyses, we tested for normality of residuals, homoscedasticity of errors, independence or errors, absence of influential points and absence of outliers to check whether our data met the assumptions of regression analyses. In rare cases where data appeared to consist of two clouds of points, relationships were also tested using Spearman's correlation coefficient. For the multiple regressions, predictor variables were selected as to not violate the assumption of collinearity among them and we tested the absence of (multi)collinearity. We selected the most parsimonious multiple regression models using Akaike information criteria (AIC). For linear mixed models, we tested the homogeneity of the variances using a Levene's test and the residuals for normality with a Shapiro test. Litter mass loss data were In-transformed to improve normality. All statistical analyses were performed in R version 3.0.2 (R Development Core Team 2013) using the lme4 package for mixed models (Bates & Maechler 2009) and the lmerTest package to calculate P-values (Kuznetsova, Brockhoff & Christensen 2013). We used Satterthwaite's approximation to calculate the denominator degrees of freedom (SAS Institute Inc., 1978).

Results

MASS LOSS AND HOME-FIELD ADVANTAGE

Litter mass loss was significantly affected by source vegetation type, source elevation, incubation vegetation type and incubation elevation (Table 1). In general, meadow and *Salix* litter decomposed faster than heath litter; this was especially the case for litter sourced from lower elevations, as indicated by the significant interaction between source vegetation type and source elevation (Table 1; Fig. 1). In

Table 1. The influence of source vegetation ('source veg'), source elevation ('source elev'), incubation vegetation ('inc veg') and incubation elevation ('inc elev'), and their interactions, on litter mass loss tested in a general linear mixed model

	F	d.f.*	P
Source veg	257.1	2	< 0.001
Source elev	30.2	2	< 0.001
Inc veg	10.0	2	< 0.001
Inc elev	62.2	2	< 0.001
Source veg × source elev	23.0	4	< 0.001
Source veg × inc veg	1.0	4	0.401
Source elev × inc veg	0.5	4	0.703
Source veg × inc elev	1.8	4	0.131
Source elev × inc elev	0.1	4	0.990
Inc veg × inc elev	5.4	4	< 0.001
Source veg \times source elev \times inc veg	0.9	8	0.557
Source veg \times source elev \times inc elev	0.7	8	0.660
Source veg \times inc veg \times inc elev	0.6	8	0.816
Source elev \times inc veg \times inc elev	0.4	8	0.936
4-way interaction	0.7	16	0.834

Values in boldface represent significant effects with P < 0.001. F = F-value, d.f. = degrees of freedom, P = P-value.

^{*}Denominator d.f. = 320 (estimated with the Satterthwaite method).

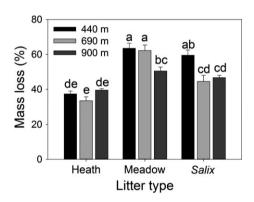


Fig. 1. Mean litter mass loss (%) \pm SE per litter type, that is, each bar represents the mean litter mass loss of that litter type across all sites in which it was incubated (N=5). Bars topped by the same letter are not significantly different at P<0.05 (Tukey's *post hoc* test).

addition, litter was generally decomposed faster at lower elevations (Fig. 2). This effect was stronger for heath and meadow vegetation where litters decomposed faster at the 440 m than at the 690 m and 900 m elevations, than for the *Salix* vegetation where litters decomposed at similar rates between the elevations. This result was supported by a significant interactive effect between incubation elevation and incubation vegetation type (Table 1; Fig. 2).

There were no significant interactions between source vegetation type or source elevation and incubation vegetation type or incubation elevation, indicating that there were no interactions between the origin of the litter substrate and the incubation environment and therefore no HFA effects (Table 1). Further, the ADH index (percentage of additional decomposition at home as compared to

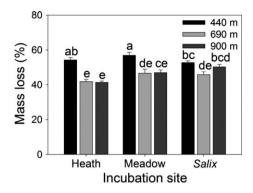


Fig. 2. Mean litter mass loss (%) \pm SE per incubation site, that is, each bar represents the mean litter mass loss of all different litter types in that incubation site (N=5). Bars topped by the same letter are not significantly different at P < 0.05 (Tukey's *post hoc* test).

Table 2. The influence of vegetation type and elevation on the additional decomposition at home (ADH) tested in a general linear mixed model

	F	d.f.*	P
Vegetation	0.1	2	0.908
Elevation	2.4	2	0.104
Vegetation × elevation	0.5	4	0.765

F = F-value, d.f. = numerator degrees of freedom, P = P-value. *Denominator d.f. = 32 (estimated with the Satterthwaite method).

all away sites) was not affected by vegetation type, elevation or their interaction (Table 2) and was not significantly different from zero (t = 1.33, d.f. = 44, P = 0.191).

PLANT TRAITS AND ENVIRONMENTAL VARIABLES

Plant traits and environmental variables differed between vegetation types. Generally, when compared with the meadow and Salix vegetation, heath vegetation had plant functional traits that are more associated with resource conservations strategies (e.g. thicker leaves and low leaf nutrient concentration), and soils with lower pH, N availability and bacterial abundance, and higher fungal abundance (Tables S1 and S2, Supporting information). The effects of elevation on plant functional traits and environmental variables often varied between vegetation types (as indicated by vegetation × elevation interactions; Tables S1 and S2, Supporting information); for example, SLA increased with elevation in heath vegetation but decreased in meadow and Salix, while bacterial biomass decreased with elevation in heath and meadow vegetation, but increased in Salix. Some other variables (e.g. soil temperature and fungal biomass) decreased with elevation in all vegetation types or were unresponsive to elevation (e.g. leaf lignin content and soil nutrient availability).

RELATIONSHIP WITH PLANT TRAITS AND ENVIRONMENTAL FACTORS

Litter mass loss was significantly related to the majority of community-weighted plant foliar and litter traits. Mass loss increased with SLA and leaf and litter N and P contents, while it decreased with LDMC, leaf lignin content and leaf and litter C:N and C:P ratios (Fig. 3a-n). In contrast, none of the measured plant traits could significantly explain variation in the ADH index, indicating that variation in home-field effects was not related to variation in plant foliar or litter quality (Fig. 3o-bb). Multiple regression analyses revealed that no model containing more than one predictor was a better predictor of mass loss than the best model containing only one predictor, and that no model could explain significant variation in the ADH index, according to AIC criteria.

Litter mass loss was significantly related to many of the measured environmental factors. Mass loss increased with soil temperature, pH and soil NH₄-N concentration, while it decreased with soil moisture content, soil organic matter content, fungal:bacterial ratio, soil N content, soil C:N and C:P ratios (Fig. 4a-o). In contrast, of all the environmental variables considered, only soil P content was significantly related to the ADH index, with increased home-field advantage at low soil P content (Fig. 4o-dd). Multiple regression analyses with AIC selection criteria revealed that the best model for predicting mass loss contained two variables, namely soil temperature and soil C:N ratio ($R^2 = 0.58$, P < 0.001), while for ADH, no model containing more than one predictor was a better predictor of mass loss than the best model containing only one predictor.

Discussion

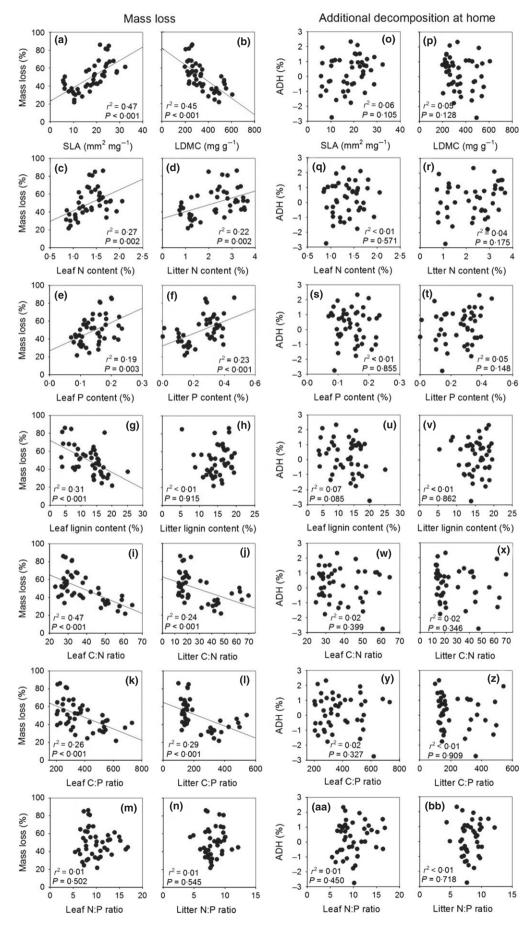
Even though we found that both litter quality and climate are important drivers of leaf litter decomposition at the whole community level, which is in line with other studies (Quested et al. 2007; Fortunel et al. 2009; Jackson, Peltzer & Wardle 2013), these factors were unimportant in determining home-field advantage (HFA) in the subarctic system that we studied. Moreover, the occurrence of HFA appears to be limited across the range of climatic conditions and vegetation types that we considered.

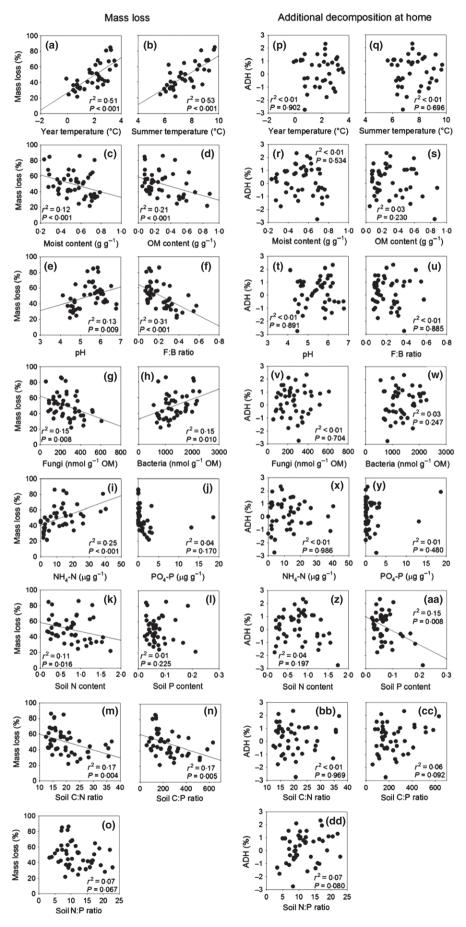
VEGETATION TYPE AND PLANT TRAITS

In contrast to our first hypothesis predicting that HFA would be stronger for vegetation types which produce litter that is more recalcitrant (Ayres et al. 2009; Milcu & Manning 2011), we found that there was no interaction between litter source and incubation environment and that home-field effects did not differ between the three vegetation types. This means that home-field effects were on average neutral and that any variation in these effects cannot be explained by vegetation type. Moreover, although plant foliar and litter traits were strong predictors of litter mass loss at the community level (Figs 1 and 3, Quested et al. 2007; Fortunel et al. 2009), they were unable to predict the direction and magnitude of home-field effects, indicating that litter quality does not serve as a driver of HFA in our study system. Our findings provide evidence that predicted increases in shrub cover in subarctic tundra due to global change (Cornelissen et al. 2007; Wookey et al. 2009) will affect ecosystem processes primarily through overall declines in community-level litter quality (Cornelissen et al. 2007), and not via decoupling of litter types from their specialized decomposer communities (Berg et al. 2010; Morrien et al. 2010) or through changes in the functional capacity of the decomposers in the soil (van der Putten et al. 2009; Cleveland et al. 2014).

These results are in contrast to previous studies that have found functional differences between microbial decomposer communities (Strickland et al. 2009a; Keiser et al. 2011), and those that have shown HFA to be more pronounced when recalcitrant litter types are involved (Milcu & Manning 2011; Wallenstein et al. 2013) and when environments being compared differ greatly in litter input quality (Strickland et al. 2009b; Freschet, Aerts & Cornelissen 2012; Veen et al. 2015). According to those studies, HFA should have been strong for litter transplants between the heath and the other vegetation types because of large differences in plant functional traits and the chemical composition of their litters (Table S1, Supporting information, Sundqvist, Giesler & Wardle 2011; Sundqvist et al. 2012). This is because plant functional traits are often strong drivers of saprophytic communities, both in tundra (Eskelinen, Stark & Männistö 2009; Sundqvist et al. 2011) and elsewhere (Hättenschwiler & Vitousek 2000; Scheu et al. 2003; Wardle et al. 2004). Further, our PLFA analyses confirm that heath vegetation with more recalcitrant litter was dominated by fungal-based microbial

Fig. 3. Litter mass loss (left panels) and additional decomposition at home index (ADH; right panels) for the whole plant community plotted against community-weighted plant leaf and litter functional traits: (a,o) specific leaf area (SLA), (b,p) leaf dry matter content (LDMC), (c,q) leaf N content, (d,r) litter N content, (e,s) leaf P content, (f,t) litter P content, (g,u) leaf lignin content, (h,v) litter lignin content, (i,w) leaf C:N ratio, (j,x) litter C:N ratio, (k,y) leaf C:P ratio, (l,z) litter C:P ratio, (m,aa) leaf N:P ratio and (n,bb) litter N:P ratio. Each dot represents an observation for one plot (N = 45 plots), and lines represent regression lines which are plotted for significant relationships only. Litter mass loss data in panels a, c, d, g, h, i, j, k and l were ln-transformed prior to calculation of correlation coefficients to achieve a normal distribution of residuals. We present untransformed data in the figures for easy interpretation of the data and for consistency. For panels f, j and l, where data appeared to consist of two clouds of points, Spearman's r was 0.48 (P < 0.001), -0.49 (P < 0.001) and -0.51 (P < 0.001), respectively.





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Fig. 4. Litter mass loss (left panels) and additional decomposition at home index (ADH; right panels) for the whole plant community plotted against environmental variables: (a,p) average soil temperature, that is across the whole litter incubation period, (b,q) average summer soil temperature, that is across the snow-free months June, July, August and September, (c,r) soil moisture (moist) content, (d,s) soil organic matter (OM) content, (e,t) pH, (f,u) ratio of fungal: bacterial PLFAs, (g,v) fungal biomass, (h,w) bacterial biomass, (i,x) soil NH₄-N, (j,y) soil PO₄-P, (k,z) total soil N content, (l,aa) total soil P content, (m,bb) soil C:N ratio, (n,cc) soil C:P ratio and (o,dd) soil N:P ratio. Each dot represents an observation for one plot (N = 45 plots), and lines represent regression lines which are plotted for significant relationships only. Litter mass loss data in panels c, d, e, i, k and l were ln-transformed prior to calculation of correlation coefficients to achieve a normal distribution of residuals. We present untransformed data in the figures for easy interpretation of the data and for consistency.

communities which are mostly well adapted for degrading recalcitrant compounds and associated with slow recycling of nutrients, while meadow and Salix vegetations were dominated by bacterial-based communities that are better adapted for degrading more labile compounds and are associated with a fast recycling of nutrients (Wardle et al. 2004; van der Wal et al. 2013). Even though these vegetation types appear to have dissimilar microbial communities (Table S2, Supporting information), this was not reflected in our HFA data. We emphasize however that while PLFA measures inform on microbial community composition, a better understanding of how the functional capacities of microbial communities associated with different vegetation types help drive HFA would require a more detailed assessment of their functional (including enzymatic) capabilities.

The lack of HFA between the vegetation types in our study (Table 1) may be because, in contrast to the majority of studies on home-field effects, our litter consists of a mixture of several coexisting plant species with contrasting qualities, each potentially experiencing different home-field effects (Perez et al. 2013). As such, while our communitylevel approach accounts for complex environmental conditions and species interactions that occur in natural ecosystems, it can mask very local-scale HFA effects that occur at the species level (Giesselmann et al. 2011; Austin et al. 2014) where neighbouring plants may promote contrasting decomposer communities that are each adapted to break down their own litter (Freschet, Aerts & Cornelissen 2012). Moreover, high-quality carbon sources in litter or the environment may promote the breakdown of recalcitrant fractions (Klotzbucher et al. 2011). Alternatively, HFA may be lacking when nutrient-limited decomposer communities in low-quality environments respond strongly to the input of labile litter from elsewhere, while at the same time, the decomposition of recalcitrant litter may be primed by the presence of labile litter in high-quality environments (Gartner & Cardon 2004; St John, Orwin & Dickie 2011). Finally, microbial communities are known to be extremely flexible and may quickly adapt to new litter inputs (Allison & Martiny 2008) potentially resulting in limited HFA in the long term.

CLIMATE AND SOIL PROPERTIES

In contrast to our second hypothesis predicting that HFA would be stronger for litter from higher elevations, we

found that the interaction between source elevation and incubation elevation did not influence mass loss and that home-field effects did not differ among the three elevations (Tables 1 and 2). Moreover, soil temperature and other soil biotic and abiotic properties generally did not explain variation among plots in home-field effects, which indicates a limited role of environmental conditions as drivers of HFA in subarctic tundra (Fig. 4). Our results therefore contrast recent findings of a variation in the functioning of decomposer communities across an elevational gradient in the Appalachian Mountains, USA (Keiser, Knoepp & Bradford 2013), but agree with other studies showing that the degree of specialization between decomposer communities does not differ across contrasting climatic conditions (Makkonen et al. 2012; Allison et al. 2013). Our results are also broadly in line with the available evidence suggesting that home-field effects, and thus the degree of specialization of the decomposer community, are largely independent of variation in climate conditions and soil properties (Veen et al. 2015). Therefore, while the predicted increase in temperature in subarctic tundra during this century (IPCC 2013) and concurrent changes in soil properties are likely to have important direct effects on decomposition rates (Figs 2 and 4, Hobbie 1996; Aerts 1997; Trofymow et al. 2002; Salinas et al. 2011; Sundqvist, Sanders & Wardle 2013), they are unlikely to alter decomposition processes by decoupling relationships between plants and specialized decomposer communities (Makkonen et al. 2012; Cleveland et al. 2014).

Conclusion

We found that the occurrence of home-field advantage in subarctic tundra is limited and factors that are well recognized as drivers of litter decomposition rate did not play major roles in determining the magnitude and direction of home-field effects in our study system. These results have several implications. First, they provide evidence that, at least in our study system, the dominant vegetation types do not select for microbial communities that preferentially decompose their own litter. Therefore, the influence of historical resource conditions on the functioning of microbial communities sometimes observed in other ecosystems (Strickland et al. 2009b; Keiser et al. 2011; Keiser, Knoepp & Bradford 2013) may not apply in relatively unproductive or low-temperature environments such as subarctic tundra. Secondly, the lack of HFA suggests that the release of nutrients from litter is not accelerated at

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Data accessibility

Environmental data and litter mass loss data are deposited in the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.rh460) (Veen, Sundqvist & Wardle 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

- **Table S1.** Mean community-level green leaf and litter traits (\pm SE) for each vegetation type at each elevation (upper sub-table) and the effect of vegetation type and elevation on green leaf and litter traits tested in a 2-way ANOVA (lower sub-table).
- **Table S2.** Mean value for environmental variables (\pm SE) for each vegetation type at each elevation (upper sub-table) and the effect of vegetation type and elevation on environmental variables tested in a 2-way ANOVA (lower sub-table).