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Exploring drivers of litter decomposition in a greening Arctic: Results from a transplant experiment across a tree-line

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Abstract

Decomposition of plant litter is a key control over carbon (C) storage in the soil. The biochemistry of the litter being produced, the environment in which the decomposition is taking place, and the community composition and metabolism of the decomposer organisms exert a combined influence over decomposition rates. As deciduous shrubs and trees are expanding into tundra ecosystems as a result of regional climate warming, this change in vegetation represents a change in litter input to tundra soils and a change in the environment in which litter decomposes. To test the importance of litter biochemistry and environment in determining litter mass loss, we reciprocally transplanted litter between heath (*Empetrum nigrum*), shrub (*Betula nana*) and forest (*Betula pubescens*) at a sub-arctic tree-line in Sweden. As expansion of shrubs and trees promotes deeper snow, we also used a snow fence experiment in a tundra heath environment to understand the importance of snow depth, relative to other factors, in the decomposition of litter. Our results show that *B. pubescens* and *B. nana* leaf litter decomposed at faster rates than *E. nigrum* litter across all environments, while all litter species decomposed at faster rates in the forest and shrub environments than in the tundra heath. The effect of increased snow on decomposition was minimal, leading us to conclude that microbial activity over summer in the productive forest and shrub vegetation is driving increased mass loss compared to the heath. Using *B. pubescens* and *E. nigrum* litter, we demonstrate that degradation of carbohydrate-C is a significant driver of mass loss in the forest. This pathway was less prominent in the heath, which is consistent with observations that tundra soils typically have high concentrations of 'labile' C. This experiment suggests that further expansion of shrubs and trees may stimulate the loss of undecomposed carbohydrate-C in the tundra.

48 *Introduction*

49 Climate warming in the Arctic of 1 – 4 °C since 1960 (Serreze and Francis 2006,
50 Serreze and Barry 2011) has resulted in large areas of tundra becoming more
51 productive, with some landscapes showing increases in aboveground biomass of 10 g
52 m^{-2} yr^{-1} (Epstein et al. 2012). In many of these areas, shrubs and trees have been
53 observed to increase in cover and height (Myers-Smith et al. 2011, Elmendorf et al.
54 2012) and are generally thought to contribute to the increase in "greenness" that is
55 observed from space (Tape et al. 2006). Earth system models have predicted that
56 increased productivity in arctic ecosystems will increase carbon (C) sequestration at the
57 biome level (Cramer et al. 2001, Qian et al. 2010, Todd-Brown et al. 2013) through
58 increased litter-fall. However, these predictions are at odds with observations in the
59 Arctic of lower soil organic matter (SOM) storage under shrub and tree species than
60 adjacent tundra systems (Wilmking et al. 2006, Hartley et al. 2012, Parker et al. 2015).
61 This suggests that we do not yet fully understand the interactions between plant
62 functional types (PFTs), litter input and decomposition rates and ecosystem carbon
63 cycling in the Arctic.

64 Plant litter is the primary input of C into soil (Aber and Melillo 2001); its
65 decomposition contributes towards humic substances which can lead to the formation of
66 stable soil organic matter (SOM) (Melillo et al. 1989, Sollins et al. 1996). Along with
67 physico-chemical environmental controls (i.e. temperature, humidity, pH, mineralogy),
68 the species identity and functional type are key to determining the rate of
69 decomposition of their litter and eventual contribution to SOM (Dorrepaal et al. 2005,
70 Cornelissen et al. 2007, Cornwell et al. 2008, Brovkin et al. 2012). More specifically,
71 the chemical composition of litter is important in determining its decomposition in any
72 given environment (Coûteaux et al. 1995) with low carbon: nitrogen and high cellulose:

lignin content favoring faster decomposition (Melillo et al. 1989). The decomposition of litter can be highly dependent on the interaction between litter species identity and the decomposer environment (Freschet et al. 2012, Keiser et al. 2014). Understanding the decomposition of different litter types in relevant contrasting environments will give insight into how litter decomposition may be altered under future global change.

Empetrum nigrum is widespread across arctic and alpine tundras of Fennoscandia and boreal forests across Eurasia (Bell and Tallis 1973, Tybirk et al. 2000, Büntgen et al. 2014). Decomposition of *E. nigrum* leaf litter is very slow due to its production of allelopathic compounds (Wardle et al. 1998, Gallet et al. 1999) and high concentrations of the lipid polymer cutin, which is particularly slow to break down (Tegelaar et al. 1989, Rasse et al. 2005) as a result of a well-developed waxy cuticle (Bliss 1962, Hetherington et al. 1984). In addition, its physical structure (small, needle-like leaves with low specific leaf area (Tybirk et al. 2000, Kleyer et al. 2008, Kattge et al. 2011)), is also likely contribute to slow decomposition in the field. By contrast, leaf litter of deciduous shrubs and trees decomposes faster than that of evergreen species such as *E. nigrum* (Aerts et al. 2006, Cornwell et al. 2008, McLaren et al. 2017). Litter inputs are also known to stimulate the decomposition of SOM (Subke et al. 2004), in particular, high quality litter inputs from deciduous boreal systems are linked to faster biogeochemical cycling and lower soil carbon stocks than evergreen systems (Melvin et al. 2015). A replacement of ericaceous evergreen species with deciduous shrubs and forests could thus stimulate litter decomposition and eventually higher turnover of SOM.

Previous work at the arctic tree-line has found that local site characteristics – specifically, the presence or absence of forest cover – exerted the strongest control on the decomposition of *B. pubescens* leaf litter, with higher rates of decomposition in

98 birch forests than nearby tundra heaths (Sjögersten and Wookey 2004). This vegetation
99 contrast was apparently more important than differences in regional climate (in contrast
100 to the findings of other studies; Dorrepaal et al., 2005; Cornelissen et al., 2007) and
101 experimental warming. The authors hypothesized that litter moisture in the birch forest
102 was important in enhancing decomposition rates, but other abiotic factors such as
103 deeper snow cover and therefore warmer winter soils and more active microbial
104 communities (Grogan and Jonasson 2006, Blok et al. 2016) could also contribute to
105 this. Contrasting decomposition rates between forest and tundra sites may therefore
106 reflect the combined influence of several factors, both biotic and abiotic, the
107 disentangling of which remains challenging.

108 Saprotrophic fungi that grow in litter horizons of forest floors have the capacity to
109 degrade a large range of simple and complex plant-derived structural molecules and are
110 therefore key to the decomposition of litter (Hatakka 1994, Rytioja et al. 2014, Talbot et
111 al. 2015). Decomposition in tundra soils, by contrast, may be under different controls,
112 where strong environmental pressure, such as low temperature (Robinson 2001) and a
113 'closed' C and N cycle dominated by ericoid mycorrhizal fungi (Read and Perez-
114 Moreno 2003), may restrict the growth and activity of other fungi. A comparison of the
115 components of soil C in forest and tundra heath supports this view, showing that tundra
116 has a more 'labile' signature, with more poorly-decomposed, cellulose-related fractions
117 than the soil of mountain birch forest (Sjögersten et al. 2003). This would suggest that
118 there is less fungal activity in the tundra, especially that of 'brown-rot' fungi which
119 target cellulose as their primary energy source (Talbot et al. 2015). An expansion of
120 forests could result in increased metabolism of previously poorly-decomposed litter
121 should the appropriate decomposer community become present.

Using a decomposition experiment whereby litter from the dominant species of three important vegetation types (forest, shrub and tundra heath) was reciprocally transplanted across a sub-arctic tree-line, we aimed to understand the key drivers of decomposition rates in this ecosystem. We tested the following specific hypotheses:

1. Litter from the more productive vegetation types (forest and shrub) decomposes at the fastest rates, regardless of the local soil environment;
2. The forest and shrub environments are more favorable than tundra heath for the decomposition of all litter types, irrespective of origin;
3. Deep winter snow and associated soil microclimates, which are characteristic of forest and shrub environments, increase litter decomposition compared to heath environments.

1344. *Materials and methods*

135 *Sites description*

136 The study area spans a 2 km^2, permafrost-free landscape around the sub-arctic/alpine
137 tree-line at Nissunsnuohkki (Abisko area, Sweden; ca. 68°18'N 18°49' E, ~600 m asl).
138 The tree-line is formed by mountain birch (*Betula pubescens* Ehrh. ssp *czerepanovii*
139 (Orlova) Hämet Ahti), with an ericaceous understorey, and the ecotone typically
140 comprises of a thick layer of shrub vegetation before transitioning to tundra heath
141 dominated by *Empetrum nigrum* L. ssp *hermaphroditum* (Hagerup) Böcher and
142 *Vaccinium vitis-idaea* L. The intermediate shrub zone is dominated by *Betula nana* L.
143 and grey willow (*Salix*) species (typically *Salix glauca*, often accompanied by *Salix*
144 *lanata*; other *Salix* spp., including *S. hastata* and *S. lapponum*, occur less frequently).
145 Soil pH in the organic horizon is 4.5 ± 0.1 at forest and 4.3 ± 0.1 at heath locations in
146 the Abisko area (Table 1). Twelve independent, short (<100 m) transects were
147 established across the multiple forest patches in the tree-line study area. Transect
148 lengths ranged from 52 to 97 m depending on the sharpness of the forest - heath ecotone
149 transition. The soils at all sites are well-drained (Sjögersten and Wookey 2002) with
150 standing-water only observable for a short number of days every year at snow melt
151 (Parker, Personal Observation). Care was taken to select vegetation transitions that were
152 not influenced by local topography, for example where water and snow accumulation
153 due to dips and hollows dominate site conditions, and avoiding steep slopes (mean
154 elevation change from heath to forest plots of 2.7 m). For more details on study sites,
155 see Parker et al. (2015).

156 Three plots (approximately 2 m^2) were established along each transect in order to
157 represent the transition in vegetation from heath to forest. These were designated:

158 tundra heath (H), shrub (S) and forest (F) (see Table 1 for further plot details). H plots
159 were chosen for an open heath environment with low *B. nana* cover and a low canopy
160 height, and with vegetation dominated by *E. nigrum*. S plots were identified as areas
161 dominated by *B. nana* with shrub height characteristically between 40 and 60 cm. F
162 plots were chosen to be in areas dominated by *B. pubescens*, approximately 10 to 15 m
163 inside the forest edge.

164 *Snow fences and snow depth measurements*

165 Five replicate 3.5 m wide, 1.5 m high snow fences were erected on tundra heath sites
166 between 0.1 and 1 km north of the transect sites (Fig. S1). They were erected before
167 snowfall in 2012 and in 2013 (and lowered during the summer to avoid shading the
168 vegetation and influencing evapotranspiration), and designed to create snow drifts of
169 comparable depth to the typical seasonal snow-cover at F and S plots on the transects.
170 To replicate the snow at F plots, plots were set up 2 m to the leeward side of the fence,
171 7 m for the S plots and 20 m for the H plots (no extra snow). Snow depths were
172 measured at both snow fence and transect plots, once each between 14/3 and 29/3 in
173 2013 and between 29/3 and 30/3 in 2014. At each of the transects, snow depth was
174 recorded at five points taken within 1.5 m of the logged position of the litter bags (the
175 horizontal accuracy of the GPS unit was 3 m). At the snow fences this was not
176 necessary due to the exact known location of the litter bags under the snow, and one
177 measurement was taken per plot. The snow fence treatment that replicated shrub snow
178 depths increased snow depths by 17 cm (compared to 19 cm in the shrub sites). The
179 snow fence plots that replicated snow found in the forests increased snow depth by 55
180 cm (compared to 46 cm in the forest sites (Table 1)).

181

Litter bags

Litter was collected from four different transects at the Abisko study site from 2/9/2012- 12/9/2012. Freshly fallen *B. pubescens* and *B. nana* litter was collected from the top of the litter layer, taking care to exclude older litter (which was easily identified). *E. nigrum* litter was collected by carefully removing senesced leaves from the stem of extracted *Empetrum* shoots. Only recently senesced leaves were taken (light brown colour, 2-4 years old according to growth scars). Litter was collected from the 'home' plots in which each species is dominant; i.e. *B. pubescens* from F plots, *B. nana* from S plots, and *E. nigrum* from H plots. All litter was sorted to remove any adhering particles or litter from other species, and air dried at 40°C for 72 hours. For each species, 0.5 ± 0.01 g of litter was weighed into 7 x 7 cm polyester mesh bags with a 0.3 mm mesh size and heat sealed. Note that the relatively small mesh size required to contain the *E. nigrum* litter will exclude many soil and litter fauna. All litter bags were placed in the field on 17/9/2012. Six bags of each species were placed at every plot on all 12 transects and at snow fences. Care was taken to ensure that every bag had good contact with the L horizon at each plot. Two corners of each bag were fastened to the ground using stainless steel pins and all bags were tied with nylon thread to nearby vegetation. Bags were also deployed in the same manner on the leeward side of the snow fences. Ten additional 0.5-g samples of each species were oven dried at 60°C for 72 hours, and the mass of undecomposed litter at the initiation of field emplacement was corrected according to the residual moisture of air-dried litter.

On 13/6/2013 (269 days of incubation), 24/7/2013 (310 days), 16/9/2013 (365 days), 20/6/2014 (641 days) and 18/10/2015 (1126 days) one litter bag of each species (one to two on the final harvest, see later text)) at each plot at both transect and snow fence sites was retrieved from the field and oven dried at 60°C for 72 hours. Once ingrown

vegetation was removed, the remaining litter was extracted, weighed, and percentage mass remaining calculated. Due to the duration of field emplacement (>3 years) some litter bags were lost or disturbed (9.8 %); at the final harvest, if two bags were remaining at a plot and both bags were not damaged, a mean percentage remaining of the two was calculated.

Solid state CPMAS ^{13}C NMR

Five samples of *B. pubescens* and *E. nigrum* in either the H or F sites at the 641-day harvest were taken forward for solid state ^{13}C nuclear magnetic resonance CPMAS ^{13}C NMR (cross-polarization/magic angle spinning ^{13}C nuclear magnetic resonance spectroscopy) and elemental (C and N) analysis. Samples were randomly selected within each of the four groups Samples were randomly selected from a pool of 12 samples within each of the four groups (species (*B. pubescens, E. nigrum*) and site (Forest, Heath) combinations). For both species, three randomly selected undecomposed litter samples (from a pool of ten undecomposed samples at the beginning of the experiment) were taken forward for CPMAS ^{13}C NMR. This totalled 26 samples taken for CPMAS ^{13}C NMR. *Betula pubescens* and *E. nigrum* was selected for the for CPMAS ^{13}C NMR analysis as they had the most contrasting decomposition rates.

CPMAS ^{13}C NMR spectra were obtained using a Bruker Avance 300 spectrometer (Bruker Analytik GmbH, Rheinstetten, Germany). 2500 scans were obtained from approximately 0.25 g of ball-milled leaf material of each sample, packed into a cylindrical zirconia rotor with approximately 0.02 g Tetrakis (trimethylsilyl) silane (TKS) packed on top and sealed with a Bruker Kel-F drive cap (Bruker Analytik GmbH, Rheinstetten, Germany). The scanning parameters were as follows: 200 MHz

231 frequency, 1000 ms contact time, 1.5 s relaxation time, 5500 Hz spinning speed, and
232 line broadening of 50 Hz. Chemical shift values were obtained compared to TKS. Total
233 signal intensities from NMR spectra were integrated into eight major chemical shift
234 regions (Table 3).

235

236 *FTIR-NMR spectra transformation*

237 Diffuse reflectance Fourier transform infrared (FTIR) spectroscopy in combination with
238 multivariate statistical techniques represents a robust and low-cost way of predicting
239 major properties of various materials including NMR-observed chemistry
240 (Forouzangohar et al. 2015). We applied FTIR spectroscopy to build a predictive model
241 from the 26 samples with NMR spectra. This model was later used to predict change in
242 litter organic chemistry for the final harvest. For these 26 samples, FTIR spectra were
243 acquired on a Bruker Vertex 70 (Bruker Optics, Billerica, MA, USA) equipped with a
244 wide-range Si beam splitter and mid infrared detector with Csl windows and a Pike
245 Autodiff (Pike Technologies, Madison, WI USA) diffuse reflectance accessory for
246 finely ground samples from undecomposed and 641-day harvests which already had
247 associated NMR spectra (n = 26), as well as on 20 samples from the 1126-day harvest
248 that did not have associated NMR spectra. Consistent with the sample selection for
249 NMR, 5 replicates of each treatment were randomly selected from the 1126-day harvest
250 (n = 20). Spectra were acquired on finely ground material over 6000-180 cm^{-1} with a
251 resolution of 4 cm^{-1}. For each sample, 60 scans were collected and averaged using the
252 OPUS software package (Bruker Optics) and then corrected for background signal
253 (average of 60 scans) and transformed into absorbance spectra.

The acquired FTIR spectra were truncated to 4000-630 cm^{-1} and normalized using the standard normal variation (SNV) transformation. A partial least squares regression (PLSR) analysis was used to predict the eight major NMR chemical shift regions on the 26 samples that had associated NMR data. Given the small sample size (n = 26), a full cross-validation procedure was used. The PLSR analysis was able to produce good 5-factor models for the dominant chemical shift regions, with less reliability for the regions with only minor contributions (Table S1). These models were then used to predict the signal intensity in each chemical shift region, along with prediction errors (De Vries & Ter Braak, 1995), for the unknown samples that decomposed for 1126 days in the field. All data processing and analysis was performed using the Unscrambler X software (CAMO Software AS, Oslo Norway). To aid in the interpretation of the ^{13}C NMR data, the distribution of signal intensity from each of the chemical shift regions (Table 3) at each time point (undecomposed, 641-day, 1126-day) was used in a molecular mixing model (Baldock et al. 2004) which calculates the best linear fit of the distribution of NMR signal intensity of five major biochemical components (carbohydrates, protein, lignin, lipids and carboxyl C).

After analysis by CPMAS ^{13}C NMR (undecomposed and 641-day), samples were separated from TKS, ensuring no contamination of the sample, and were analysed for carbon and nitrogen content after combustion in a Vario EL Cube elemental analyser (Elementar, Hanau, Germany). After FTIR analysis, the 1126-day samples were analysed for carbon and nitrogen content using a Flash 2000 CN analyser (Thermo Scientific, Waltham, MA, USA). The carbon content data were then applied to the actual mass of the litter remaining and estimated fractions of C components to calculate the mass of carbon remaining in each component.

Statistical analysis

Decay constants (*k*) were calculated for the loss of litter mass of every replicate species and site combination on both the snow fence and natural transect experiments according to the negative exponential litter decay model

$$\ln (M_t/M_0) = -kt \qquad \text{equation (1)}$$

where M_0 is the initial dry mass of the sample and M_t is the mass at time t (years). The first two harvests (269 days and 310 days) were omitted for this calculation because they do not fit the long-term exponential decay model as a result of low mass loss in the first winter. Differences in *k* between site (heath, shrub and forest (or snow level in the case of the snow fence experiment)) and species (*E. nigrum*, *B. nana* and *B. pubescens*) were compared using a linear mixed effects model in the 'nlme' package (Pinheiro et al. 2017) of the R statistical software (R Development Core Team 2016). In the linear mixed effects model, 'Transect' was expressed as a random intercept factor due to unquantified baseline differences in decomposition between transects. The interaction between 'site' and 'species' was found not to be statistically significant in the original model ($P = 0.64$) and was therefore removed from the analysis (Crawley 2007). Pairwise comparisons of decomposition rates between different levels of species and site types were carried out by comparing Least-Square means derived from the statistical models with a Tukey HSD test.

The mass remaining and the percentage of undecomposed samples remaining of carbohydrates, lipids and lignin estimated from NMR spectra were analysed using a three-way ANOVA with time, site (heath and forest) and species (*B. pubescens* and *E. nigrum*) as treatment effects. The percentage data were arcsin- square root transformed

prior to analysis. All analyses were carried out using R v3.3.1. (R Development Core Team 2016).

Results

Litter decomposition rate

Decomposition rates differed significantly between species on both the natural transects ($P < 0.001$, Table 2) and at the snow fence experiment ($P < 0.001$, Table 2). *Betula pubescens,* with an average decomposition constant of 0.25 $year^{-1}$ across all sites, decomposed significantly faster than both *B. nana* (0.18 $year^{-1}$ ($P < 0.001$)) and *E. nigrum* (0.15 $year^{-1}$ ($P < 0.001$)) (Fig. 1a), *B. nana* decomposed faster than *E. nigrum* ($P = 0.0018$). The host site (in which litter was decomposing) was also highly significantly related to decomposition rates in the litter transplant experiment ($P < 0.001$, Fig. 1a, Table 2). On average, across litter types, litter decomposed marginally faster in the forest (decomposition constant = 0.21 $year^{-1}$) than in the shrub sites (0.20 $year^{-1}$ ($P = 0.06$) and heath sites (0.18 $year^{-1}$ ($P < 0.001$)). Overall, decomposition was faster in the shrub sites than the heath sites ($P = 0.011$). There was no effect of different snow treatments on litter decomposition rates in the snow fence experiment ($P = 0.9$ Fig. 1b, Table 2). At the end of the experiment, *B. pubescens* in the forest and shrub plots had the least mass remaining (51 % each (Fig. 2)) and *E. nigrum* in the heath had the most (71 % (Fig. 2)).

^{13}C NMR and carbon components of litter

Prior to decomposition, *E. nigrum* and *B. pubescens* differed substantially in the relative contributions of different regions of their NMR spectra, with *E. nigrum* dominated by alkyl-containing compounds and *B. pubescens* dominated by O- alkyl-containing

compounds (Table 3). These initial proportional differences in NMR spectra were still apparent after litter had decomposed after 641 and 1126 days in the field (Table 3). The proportion of O-alkyl compounds in both litter types reduced through time whilst alkyls remained stable as a proportion of the litter remaining in both litter types, resulting in an increase in Alkyl:O-alkyl ratio (Table 3). The C:N ratio of fresh *B. pubescens* litter was (60.8) under half of that measured in *E. nigrum* (138.3). Over time the C:N ratio decreased rapidly for both litter types, especially in the forest plots where C:N ratio at the end of the experiment reduced to 23.6 and 50.8 in for B. pubescens and E. nigrum respectively (compared to 31.9 and 64.3 at the heath plots (Table 3)).

Prior to decomposition, litter from *B. pubescens* contained 1.7 times more carbohydrate-C than *E. nigrum*, whereas *E. nigrum* had 4.9 times more lipid-C in its biomass compared to *B. pubescens*. Amounts of lignin were similar between the litter types (Fig. 3). After incubation in the field, there was a highly significant effect of site ($F = 28$, $P < 0.001$ (Table S2)) and species of litter ($F = 26$, $P < 0.001$ (Table S2)) on the mass of carbohydrates remaining in litter, whereby this mass was lower in litter decomposing in forest plots and *B. pubescens* contained higher amounts of carbohydrates than *E. nigrum*, respectively (Fig. 3a). In the forest, litter carbohydrates initially decomposed rapidly between 0 and 614 days, and then stabilized at approximately 40 % (*B. pubescens*, Fig. S3a) and 50 % (*E. nigrum*, Fig. S3a), after which there was only marginal mass loss (Fig. 3). In contrast, the decomposition of litter carbohydrates in the heath followed a more linear pattern, with slower decomposition to 614 days, which then continued to 1126 days. The final percentage mass remaining of carbohydrates of both *B. pubescens* (49 %) and *E. nigrum* (54 %) at the end of the experiment in the heath was within 10 % and 6 %, respectively, of the litter in the forest, despite slower initial decomposition rates (Fig. S3a).

Due to very high alkyl-C contents in *E. nigrum* litter, the mass of lipids modelled to be present in this litter was also very high (Fig. 3b), resulting in a highly significant relationship between species type and mass of lipids in extracted litter samples ($F = 690$, $P < 0.001$). There was also a strong effect of site on mass of lipids, with lower amounts remaining in both *E. nigrum* and *B. pubescens* at the forest plots ($F = 15$, $P < 0.001$ (Table S2)). When expressed as a proportion of the original lipid mass, the results show a strong effect of 'species' ($F = 18$, $P < 0.001$ (Table S2)) and 'site' ($F = 12$, $P = 0.002$ (Table S2)); *B. pubescens* had 60 % of lipid mass remaining in the forest and 70 % in the heath, whereas *E. nigrum* had 82 % remaining in the forest and 96 % in the heath (Fig. S3b).

Lignin was present in low amounts in litter (Fig. 3c) and there were no significant differences in mass of lignin remaining over the study duration between site ($F = 0.4$, $P = 0.5$ (Table S2)) or species ($F = 0.0003$, $P = 0.98$ (Table S2)), but there was a significant decline in mass with time ($F = 11$, $P = 0.002$ (Table S2)). Although initial amounts of lignin were low (Fig. 3c), it decomposed in all species-site treatments to about 50 % of its original amount (Fig. S3c)

Discussion

The greater decomposition rates of *B. pubescens* and *B. nana* than *E. nigrum* regardless of decomposition environment clearly support the first hypothesis that litter from an arctic tree and shrub species decomposes at a faster rate than the typical heath species, *E. nigrum*. This difference is consistent with the differences in C stocks in the environments that these species dominate respectively i.e. low C stocks in forest and high C stocks in tundra heath (Hartley et al. 2012, Parker et al. 2015).

374 Litter of *E. nigrum*, a key species of tundra heaths, decomposed very slowly. This is
375 likely due to high levels of aliphatic compounds (alkyls) which make up the lipids of its
376 waxy cuticle (Bliss 1962, Hetherington et al. 1984). Lipid levels in *E. nigrum* litter were
377 over four times higher than in *B. pubescens*, and showed very low rates of mass loss,
378 especially in the tundra heath environment. Whilst our methods cannot distinguish
379 between plant- *vs.* microbe-derived alkyls (Baldock et al. 1997), it is clear that these
380 compounds are contributing substantially to the persistence of *E. nigrum* litter in this
381 experiment. The strong contribution of lipids to long-term SOC storage in tundra heaths
382 is also corroborated by the components of C found in the SOM of ericaceous tundra
383 around Abisko (Sjögersten et al. 2003), which also contained high levels of alkyls. This
384 link between aliphatic compounds in *E. nigrum* litter and a resulting alkyl signature in
385 the soil has also been found in Norwegian tundra heath systems (Väisänen et al. 2015),
386 emphasizing that this could be a significant driver of high SOM storage in tundra.
387 Although we could not explicitly address the potential role of the physical structure of
388 the litter studied here, it is important in determining decomposition rates (Cornelissen et
389 al. 1999). *E. nigrum* has a far lower surface area: mass ratio (Specific leaf area) than the
390 *Betula* species used in this study (Kleyer et al. 2008) which may render the substrate
391 more immediately available to decomposer communities.

392 In contrast to *E. nigrum*, *B. pubescens* lost substantial mass in the initial stages of
393 decomposition. The measurements of remaining carbon suggest that this initial rapid
394 decomposition was due to the metabolism and breakdown of the initially high levels of
395 carbohydrates (predominately O-alkyls). This loss of carbohydrates is a likely
396 contributing factor to rapid turnover of C and ultimately low storage of C in the soil in
397 deciduous arctic and boreal ecosystems (Parker et al. 2015, Melvin et al. 2015).
398 Carbohydrates in *B. pubescens* litter decomposed to a similarly low residual level in the

399 tundra as in the forest, even though their initial decomposition was not as rapid. This
400 supports the hypothesis that litter identity is central to its eventual decomposability
401 (Coûteaux et al. 1995, Cornelissen et al. 2007), irrespective of *in situ* processing rates.

402 We also examined the decomposition rates of leaf litter from *B. nana*, a shrub species
403 which has been observed to be expanding its range over arctic tundra in response to
404 climate change (Tape et al. 2006, Myers-Smith et al. 2011). This litter also lost
405 significantly more mass than *E. nigrum*, and observations of high soil C flux from these
406 shrub systems (Parker et al. 2015) may in part be explained by this more rapid leaf litter
407 turnover. However, *B. nana* decomposed at slower rates than *B. pubescens*, which could
408 be due to a number of factors including differences in specific leaf area (a facet of
409 physical structure; note earlier paragraph), N content and structural C compounds.
410 Indeed, with regards to the litter chemistry Väisänen et al. (2015) reported carbohydrate
411 concentration of 39 % and alkyl to O-alkyl ratio around 0.51 indicating that the
412 intermediate decomposition rates of *B. nana* may be attributed to its intermediate levels
413 of carbohydrates (Väisänen et al. 2015). Based on our observed species-specific
414 decomposition rates, any expansion of *B. pubescens* forests is likely to increase leaf
415 litter decomposition in tundra to a greater extent than an expansion of *B. nana,* but both
416 are likely to increase C cycling rates if only PFT (deciduous) of the litter input is
417 considered.

418 The second overarching hypothesis of this study, that litter would decompose fastest in
419 the forest and shrub environments compared with the heath, was supported by the
420 majority of the data, with the exception of the shrub *B. nana*. Our snow fence
421 experiment gives some insight into separating the influence of abiotic (snow depth,
422 temperature and, potentially, moisture) effects on decomposition from the confounding
423 biological factors (i.e. vegetation/microbial). There were no increases in litter loss with

424 increased winter snow depth over the 2 years of study, concurring with findings of
425 another study in arctic tundra (DeMarco et al. 2014) but not those of Blok et al. (2016).
426 As the experimentally manipulated snow depth did not influence decomposition rates,
427 we must conclude that the naturally deep snow cover was not the driver behind the
428 rapid decomposition which we observed in the forest. We however, do not rule out a
429 longer-term effect of many years of snow cover on microbial communities and resulting
430 decomposition rates. Litter moisture is an abiotic factor that we could not take directly
431 into account in the present study. It is known to be important in controlling microbial
432 activity and litter turnover in boreal forests (Schimel et al. 1999), and low surface
433 moisture in heath ecosystems has been implicated in slowing decomposition (Sjögersten
434 and Wookey 2004). We acknowledge that there are abiotic controls other than snow
435 depth that we have not accounted for, but conclude that the major differences in
436 decomposition that we observe along the tree-line are due to microbial and biochemical
437 differences.

438 We propose that the rapid decomposition of carbohydrate rich litter in the forest was
439 driven by two interlinked processes: Firstly, there is a rich and active fungal community
440 (especially brown-rot fungi) in the litter horizons of the forest (Lindahl et al. 2007)
441 capable of producing an array of enzymes that can target initially available cellulose-
442 related structures (Talbot et al. 2015) until this source of C is depleted. Secondly, there
443 is a biochemically favorable environment that 'primes' the decomposition of cellulose
444 in the forest plots due, in part, to the high-cellulose content of previous litter-falls.
445 Temperature (Pietikainen et al. 2005) and pH (Rousk and Bååth 2011) are important in
446 determining fungal and bacterial growth rates, but soil pH and thaw-season soil
447 temperature is remarkably similar across the study ecotones (Table 1). This leaves the
448 biochemical environment as a key remaining factor explaining why fungi may grow

449 well in the birch forests. Experimental additions of cellulose have been found to
450 increase fungal growth (Subke et al. 2004, Meidute et al. 2008) and enzyme production
451 (Talbot and Treseder 2012). Thus, it is feasible that in the mountain birch forests in the
452 present study there are tight linkages between the carbohydrate rich litter, increased
453 fungal activity and rapid turnover of C (Parker et al. 2015).

454 The production of allelopathic compounds by *E. nigrum* is a process that can have
455 ecosystem-wide influence (Wardle et al. 1998). Production of poly-phenolic secondary
456 compounds by *E. nigrum* has been linked to inhibited activity of soil fungi and animals
457 and as a result lowered decomposition rates and increased build-up of SOM (Wardle et
458 al. 1998, Tybirk et al. 2000). Slow decomposition rates of *E. nigrum* in the present
459 study may partially be due to remaining residues of allelopathic compounds on the litter
460 and in the surrounding litter in the heath. However, it should be noted that the forest
461 sites also have high cover of *E. nigrum* across the understory (Parker et al. 2015) yet
462 carbon turnover is very high compared with the heath. Although assessing the
463 importance of allelopathy across the sub-arctic tree-line is not in the scope of this work,
464 it may have important controls over decomposition.

465 *Betula pubescens* litter in the forest plots decomposed to half of its original mass within
466 18 months, with limited further mass loss for the remainder of the time in the field. This
467 is consistent with observations that the most labile components of litter are decomposed
468 initially, whilst remaining litter residue starts to form soil organic matter (Melillo et al.
469 1989, Sjögersten and Wookey 2004). This prompts the question; how is carbon
470 processed after this initial mass loss, bearing in mind that standing stocks of soil
471 organic matter are very low in these forests (Hartley et al. 2012, Parker et al. 2015)? In
472 boreal forests, ectomycorrhizal fungi (EMF) grow in the organic and mineral horizons
473 below the litter (Lindahl et al. 2007) and have been shown to be able to stimulate

474 decomposition of macromolecular complexes through the production of extracellular
475 enzymes, specifically, peroxidases (Bödeker et al. 2014, Lindahl and Tunlid 2015).
476 Although other pathways are plausible, we propose that the decomposition of litter in
477 this forest ecosystem is characterized by an initial rapid mass loss due to metabolism by
478 saprotrophic fungi and bacteria of relatively simple organic molecules e.g.
479 carbohydrates, and a subsequent steadier decomposition by EMF of the remaining more
480 complex compounds. Taken together, this could result in a thin organic soil horizon and
481 low net C storage in the ecosystem (Hartley et al. 2012).

482 This study has shown that litter of a common tundra heath species, *E. nigrum*,
483 decomposes faster in forest or shrub environments than in tundra heath, and that this
484 decomposition will be driven in the first instance by carbohydrate loss. As forests are
485 expanding in range and cover in some areas of the sub-Arctic (Tømmervik et al. 2009,
486 Rundqvist et al. 2011, Hofgaard et al. 2013) and shrubs have been observed be
487 increasing in community dominance in many locations across the arctic tundra (Tape et
488 al. 2006, Myers-Smith et al. 2011), the findings of the current study have important
489 implications for the future of arctic C stocks. If tundra heath soils, rich in less-
490 decomposed forms of C (Sjögersten et al. 2003), are colonized by deciduous forest,
491 with its associated fungal community (including EMF which are also potentially
492 efficient decomposers (Lindahl and Tunlid 2015)), then this C will be rapidly
493 metabolized and a significant part of the C currently stored in tundra heath will be
494 released to the atmosphere. This would represent a positive feedback to climate
495 warming.

496 In conclusion, the dominant litter types across the forest-heath ecotone decomposed
497 faster of litter in the most productive ecosystems. We hypothesize that this is due to a
498 carbohydrate-rich input of litter from the birch canopy and the presence of a

499 decomposer community that can metabolize this relatively labile source of C. Using a
500 snow fence experiment on tundra soils, we show that the effect of increased snow in the
501 forest compared to the heath alone is modest and that the effect of environment on
502 decomposition rates in the forest is likely exerted via microbial metabolism over the
503 summer. We raise the hypothesis that microbially-accessible litter C from tundra heath
504 species is vulnerable to decomposition should more productive deciduous species
505 further expand onto heaths, resulting potentially in a net emission of CO_2 to the
506 atmosphere.

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763

764 Table 1: Site characteristics along transects at Abisko (means ± 1 SEM, n = 12).
765 'Canopy height' refers to the actual vegetation canopy for Heath, and Shrub
766 communities, and the understorey of the Forest (where mountain birch trees - *Betula*
767 *pubescens* - comprise the canopy). Snow depths measured over transects are paired in
768 either 2013 or 2014 with snow depth data from the snow fence experiment, at plots
769 which were selected to mimic snow depth along the transect. Vegetation and soil data
770 (except temperature data) are adapted from Parker et al. (2015). Soil temperature data
771 are average seasonal temperatures at 5 cm depth across six of the twelve transects. The
772 start of each season is defined by soil temperatures deviating and remaining above
773 (Summer) or below (Winter) 0 °C.
774

	Year	Property	Heath	Shrub	Forest
Vegetation		Distance from Heath (m)		28.3 ± 2.9	67.6 ± 5.9
		Canopy height (cm)	14.7 ± 0.7	32.0 ± 2.4	19.0 ± 1.7
		B. pubescens density (trees ha^{-1})			785.0 ± 109.0
		B. nana cover (%)	21.2 ± 2.7	60.3 ± 4.8	8.0 ± 2.2
		E. nigrum cover (%)	65.4 ± 3.3	66.9 ± 4.7	45.4 ± 4.2
Soil		pH (organic horizon)	4.3 ± 0.1	4.4 ± 0.1	4.5 ± 0.1
		Organic horizon carbon (kg m^{-2})	7.0 ± 0.8	3.0 ± 0.5	2.0 ± 0.3
		Mineral horizon carbon (kg m^{-2})	2.0 ± 0.3	3.3 ± 1.3	2.5 ± 0.4
	2012-13	Summer temperature (°C)	5.4 ± 0.3	5.1 ± 0.3	5.5 ± 0.2
		Winter temperature (°C)	-3.9 ± 0.2	-1.3 ± 0.2	-1.1 ± 0.2
	2013-14	Summer temperature (°C)	6.6 ± 0.3	6.6 ± 0.6	7.1 ± 0.2
		Winter temperature (°C)	-2.5 ± 0.5	-1.0 ± 0.1	-0.2 ± 0.1
Snow	2012-13	Snow depth at transects	13.1 ± 1.8	35.4 ± 4.0	46.8 ± 3.4
		Snow depth at snow fences (cm)	13.9 ± 2.2	22.6 ± 2.9	58.5 ± 13.3
	2013-14	Snow depth at transects	14.4 ± 3.5	29.7 ± 5.3	72.2 ± 9.1
		Snow depth at snow fences (cm)	13.0 ± 1.5	39.0 ± 8.7	78.2 ± 10.4

775
776

777 Table 2: The effect of species of litter and incubation site on decomposition rate (*k*) on
778 the natural transects ('Site' represents differences both in abiotic factors (e.g. snow
779 cover, thermal and moisture regimes) and biotic factors e.g. microbial community and
780 others)) and at the snow fences (where 'Environment' initially represents differences in
781 abiotic factors associated with altered snow only).

782

783

Natural Transects

Factor	d.f.	F	*P*
Species	2,89	94.4	< 0.001
Site	2,89	13.3	< 0.001

Snow fence experiment

Factor	d.f.	F	*P*
Species	2,36	86.9	< 0.001
Snow	2,36	0.2	0.9

784

785 Table 3: Percentage contributions of chemical shift regions to ^{13}C NMR spectra, Alkyl:
786 O-Alkyl ratios and C:N ratios of litter samples of *Betula pubescens* and *Empetrum*
787 *nigrum* that were decomposing in forest or heath environments at 0 days
788 (undecomposed), 614 days and 1126 days. Error values signify ± 1 SEM (n = 5 for
789 decomposed field samples, n = 3 for undecomposed samples).

	0 days	641 days		1126 days	
		Forest	Heath	Forest	Heath
	Mean ± SE	Mean± SE	Mean± SE	Mean± SE	Mean± SE
Betula pubescens					
Alkyl (0-45 ppm)	15.5 ± 0.3	20.9 ± 1.2	18.5 ± 0.2	20.8 ± 1.4	25.8 ± 7.3
N-Alkyl/Methoxyl (45-60 ppm)	5.1 ± 0.1	6.6 ± 0.6	6.2 ± 0.1	6.6 ± 0.1	6.6 ± 0.2
O-Alkyl (60-95 ppm)	47.6 ± 0.9	38.3 ± 1.6	45.7 ± 0.7	38.3 ± 1.0	40.2 ± 4.8
Di-O-Alkyl (95-110 ppm)	11.3 ± 0.2	8.7 ± 0.5	10.4 ± 0.1	8.7 ± 0.3	8.9 ± 1.2
Aryl (110-145 ppm)	11.1 ± 0.8	11.4 ± 0.8	9.6 ± 0.3	11.3 ± 0.4	9.4 ± 0.6
O-Aryl (145-165 ppm)	4.2 ± 0.2	4.5 ± 0.8	3.6 ± 0.3	4.7 ± 0.4	3.1 ± 0.5
Amide/Carboxyl (165-190 ppm)	5.1 ± 0.3	9.5 ± 1.9	6.0 ± 0.4	9.7 ± 0.7	5.9 ± 1.1
Alkyl/O-Alkyl	0.3 ± 0.0	0.5 ± 0.0	0.4 ± 0.0	0.5 ± 0.0	0.8 ± 0.4
C:N	60.8 ± 4.3	31.5 ± 1.9	49.7 ± 0.9	23.6 ± 1.3	31.9 ± 3.2
Empetrum nigrum					
Alkyl (0-45 ppm)	43.9 ± 1.0	50.3 ± 1.7	51.6 ± 1.3	52.3 ± 2.3	54.4 ± 0.9
N-Alkyl/Methoxyl (45-60 ppm)	4.7 ± 0.2	5.0 ± 0.3	5.5 ± 0.2	6.0 ± 0.1	6.0 ± 0.1
O-Alkyl (60-95 ppm)	26.9 ± 1.0	21.4 ± 1.1	24.8 ± 0.6	21.3 ± 1.7	21.7 ± 0.5
Di-O-Alkyl (95-110 ppm)	6.2 ± 0.1	4.8 ± 0.4	5.0 ± 0.1	4.4 ± 0.5	4.4 ± 0.2
Aryl (110-145 ppm)	9.9 ± 0.1	9.6 ± 0.3	7.9 ± 0.4	8.7 ± 0.2	7.9 ± 0.1
O-Aryl (145-165 ppm)	3.9 ± 0.3	4.0 ± 0.4	2.4 ± 0.3	2.9 ± 0.1	2.4 ± 0.1
Amide/Carboxyl (165-190 ppm)	4.4 ± 0.3	4.9 ± 0.5	2.8 ± 0.6	4.3 ± 0.1	3.2 ± 0.2
Alkyl/O-Alkyl	1.6 ± 0.1	2.4 ± 0.2	2.1 ± 0.1	2.6 ± 0.4	2.5 ± 0.1
C:N	138.3 ± 3.0	74.6 ± 4.5	111.6 ± 5.0	50.8 ± 3.9	64.3 ± 3.1

790
791
792

793 *Figure Legends*

794

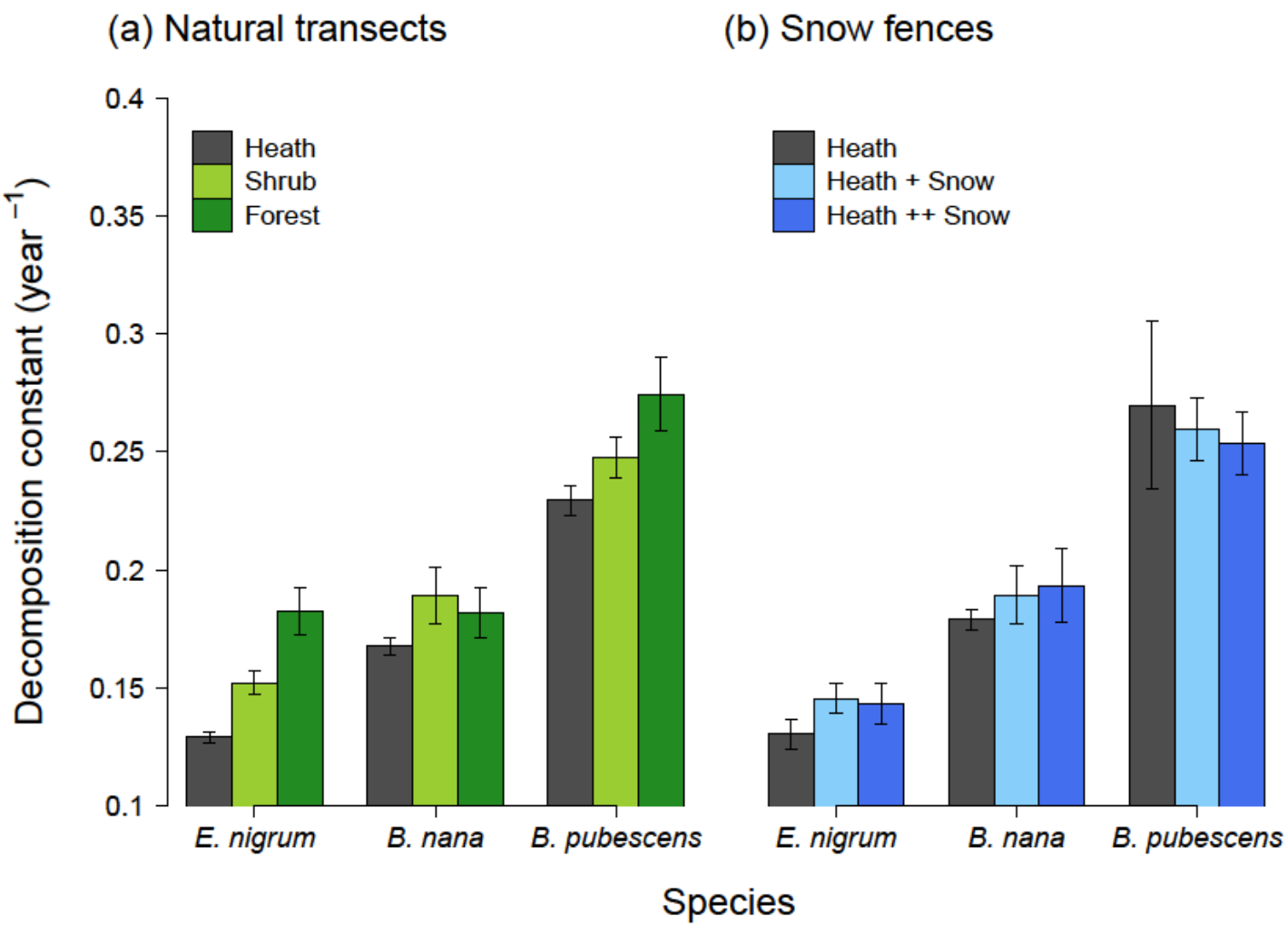
795 Figure 1: Decomposition constants (*k*) of *E. nigrum, B. nana* and *B. pubescens* litter
796 across (a) transects across natural tree-lines from heath to forest and (b) under three
797 different snow depths simulating snow accumulation found at different vegetation
798 types: Heath (control), + Snow (Shrub) and ++ Snow (Forest). Error bars represent ± 1
799 SEM (transects n = 12, snowfences n = 5).

800

801 Figure 2: Percentage mass remaining of litter over time of three different species: (a,d)
802 *Empetrum nigrum*, (b,e) *Betula nana*, (c,f) *Betula pubescens* in either distinct
803 vegetation communities (heath, shrub or forest), distributed across natural transects
804 (a,b,c), or under three different snow depths simulating snow accumulation found at
805 different vegetation types: Heath (control), + Snow (Shrub) and ++ Snow (Forest)
806 (d,e,f). Error bars represent ± 1 SEM (transects n = 12, snowfences n = 5). The extent
807 of the shaded areas on the x axis indicates the length of the snow covered season in the
808 first two years of study.

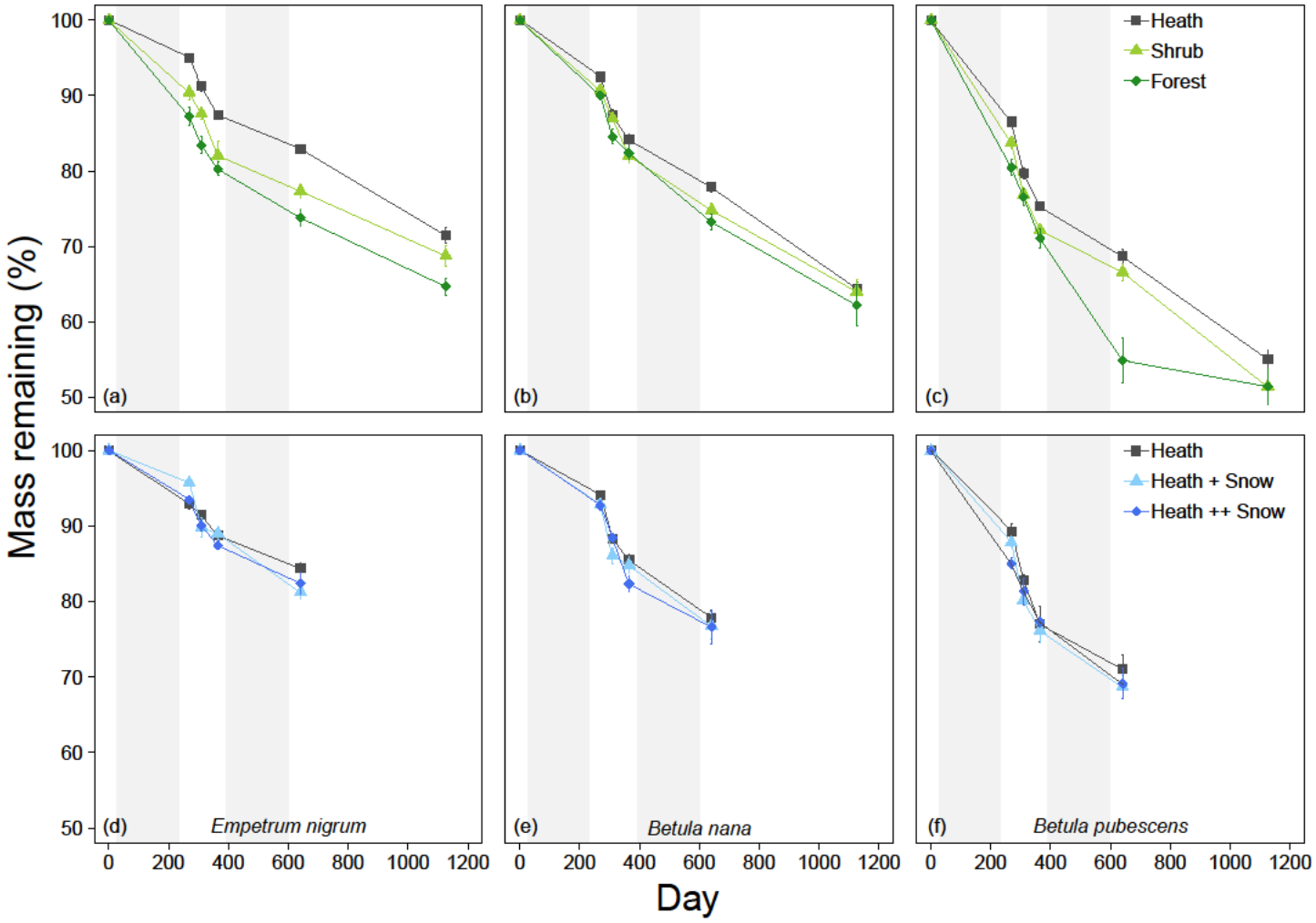
809

810 Figure 3: Mass of (a) Carbohydrates, (b) Lipids and (c) Lignin of in *Betula pubescens*
811 (green diamonds) and *Empetrum nigrum* litter (grey squares) in forest (open shapes)
812 and heath (closed shapes) environments at initial levels (0 days), and after 614 and 1126
813 days of decomposition (t5). Error bars represent ± 1 SEM (initial litter: n = 3,
814 decomposed samples: n = 5). Bold lettering in the inset text indicates significant (P
815 <0.05) factors and interactions in three way analysis of variance; number of asterisks
816 indicate level of significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, see table S2 for
817 further statistics relating to these data.


(a) Natural transects
(b) Snow fences
Heath
Shrub
Forest
Heath
Heath + Snow
Heath ++ Snow
Decomposition constant (year $^{-1}$)
0.4
0.35
0.3
0.25
0.2
0.15
0.1
E. nigrum
B. nana
B. pubescens
E. nigrum
B. nana
B. pubescens
Species

818

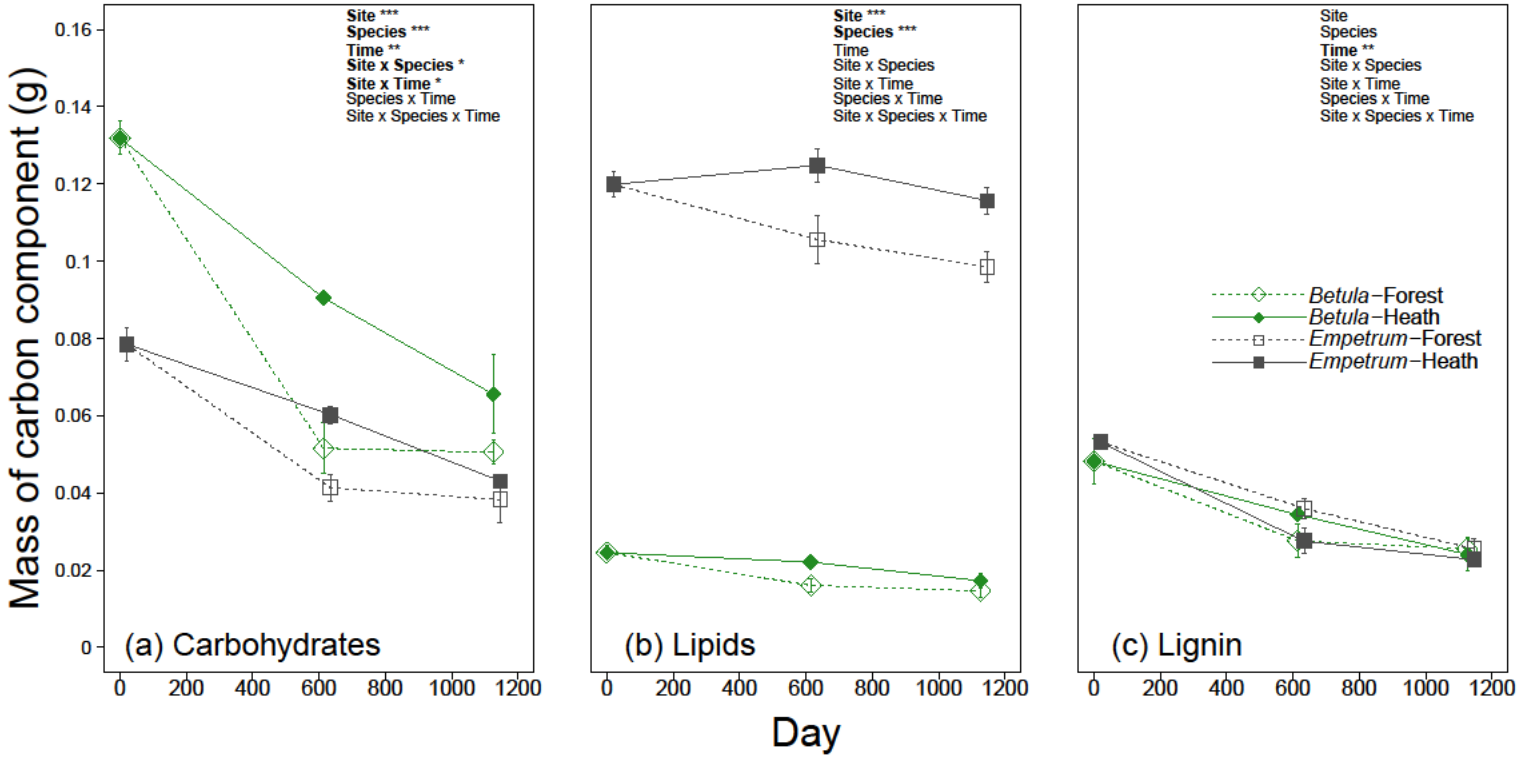
819 Fig.1


Mass remaining (%)
Day
(a)
(b)
(c)
(d)
(e)
(f)
Empetrum nigrum
Betula nana
Betula pubescens
Heath
Shrub
Forest
Heath
Heath + Snow
Heath ++ Snow
100
90
80
70
60
50
0
200
400
600
800
1000
1200

820

821 Fig.2

822



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824

825 Fig.3