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Plant community composition and an insect outbreak influence phenol oxidase activity and soil-litter biochemistry in a sub-Arctic birch-heath.

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2 **Abstract**

3 Rates of decomposition in arctic soils are regulated by temperature and moisture but substrate
4 availability is dictated by vegetation inputs, which are also subject to biotic influences. Here
5 we examine how leaf and litter inputs from individual dwarf shrub species influence soil
6 enzyme activity in a sub-arctic heath community in Abisko, Sweden. We further consider
7 how foliar damage via insect herbivory (and outbreak), affect the soil community and
8 decomposition. During the peak growing season (July 2011) we assessed how shrub
9 community composition (*Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum*
10 and *V. vitis-idaea*) determined litter and soil phenol oxidase activity. A periodic severe
11 outbreak of Autumn moth larvae (*Epirrita autumnata*) affected this community in the
12 following year (July 2012) and we used this to investigate its impact on relationships with
13 phenol oxidase activity, soil respiration, soluble NH₄⁺ and soluble phenolics; the soluble
14 factors being directly associated with inputs from insect larval waste (frass). Pre-outbreak
15 (2011), the strongest relationship observed was higher phenol oxidase activity with *E.*
16 *hermaphroditum* cover. In the outbreak year (2012), phenol oxidase activity had the strongest
17 relationship with damage to the deciduous species *V. myrtillus*, with greater herbivory
18 lowering activity. For the other deciduous species, *V. uliginosum*, soil NH₄⁺ and phenolics
19 were negatively correlated with foliar larval damage. Phenol oxidase activity was not affected
20 by herbivory of the evergreen species but there was a strong positive relationship observed
21 between *E. hermaphroditum* community abundance and soil respiration. We highlight the
22 dominant role of *E. hermaphroditum* in such sub-Arctic shrub communities and show that
23 even during insect outbreaks it can dictate soil processes.

24
25

26 **Keywords:** Arctic soil carbon, insect herbivory, *Empetrum*, *Vaccinium*, phenol-oxidase,
27 plant competition

28

29 **Introduction**

30 Biophysical constraints on organic matter decomposition have underpinned globally
31 significant accumulations of carbon (C), particularly in the organic layer of soils in northern
32 high latitude regions (Hobbie et al. 2000; Mack et al. 2004). Warmer conditions threaten
33 these stocks and could positively feedback on climate change via respired losses of C from
34 Arctic soils and litter (Dorrepaal et al. 2009). Plant communities of boreal-tundra regions
35 have characteristically low levels of primary productivity, slow rates of organic matter
36 breakdown and low rates of nutrient turnover (Flanagan and Veum 1974; Shaver and Chapin
37 1980; Hobbie et al. 2002), traits that contribute to Arctic-boreal soil C storage. These
38 communities are also sensitive to environmental change, via an ecosystem ‘cascade’ effect
39 that can develop following disturbance (Post et al. 2009; Wookey et al. 2009). Perturbed soil
40 and litter decomposition processes are the potential consequence of such cascades. Increased
41 temperatures in the Arctic are likely to alter plant community composition, with a strong
42 influence on soil C dynamics (Bardgett et al. 2013) and below-ground activity via root-
43 mycorrhizal exudate quality (Bardgett et al. 2005). Microbial-rhizosphere relationships
44 unique to each plant species (Zak and Kling 2006; van Aarle and Plassard 2010), may
45 influence below-ground functioning on a patch scale in mixed plant communities. Few
46 studies at high latitudes have examined how decomposition activity is determined by plant
47 community composition and specifically how extracellular soil enzyme activity could be
48 further modified by biotic disturbance.

49

50 Persistent episodic outbreaks of herbivory from Geometrid moth larvae affects vegetation in
51 Arctic boreal-tundra regions and is likely to impact plant-soil dynamics, yet few studies have
52 examined this. Work on temperate oak forest mesocosms, however, has demonstrated

53 increased N and C cycling following larval herbivory (Frost and Hunter 2004) Severe
54 outbreaks of moth larvae recur periodically in spring, typically following milder winter
55 conditions which boost egg viability and increase larval numbers (Tenow 1972). Such
56 episodes are, hence, expected to become more frequent as the Arctic warms (Hagen et al.
57 2007, Jepsen et al. 2008). Such herbivore episodes could short-circuit normal C cycling
58 processes via mobile nutrients introduced from dead plant material and animal waste, and
59 because in general, herbivory has been shown to impact root activity as plants recover
60 (Bardgett and Wardle 2003, Metcalfe et al. 2014).

61

62 In this study we exploited extracellular digestive enzyme activities (EEA) produced
63 by microbial organisms and plant roots in litters and soils, using these as (bio)indicators of
64 litter and soil decomposition dynamics over two growing seasons. Biotic decomposition
65 processes and microbial activity are closely coupled to EEA rates (Sinsabaugh et al. 2008)
66 and enzyme activity assays have been used widely as bio-indicators of ecological- and soil
67 biological function (Caldwell, 2005, Kardol et al. 2010). In Arctic heaths and tundra,
68 decomposing material contains high levels of phenolic compounds (Hansen et al. 2006). The
69 extracellular digestive enzyme phenol oxidase may be essential for decomposition in this
70 region because it allows access to nutrients bound in the lignin, proanthocyanidins and
71 secondary polyphenolic compounds in this organic matter (Stafford 1988; Hattenschwiler and
72 Vitousek 2000; Sinsabaugh 2010). Phenol oxidase enzymes (usually referred to singularly as
73 ‘phenol oxidase’) have been identified as the key decomposer enzyme group for common
74 peat-rich soils of northern latitudes, because phenol oxidase enables a key biochemical step
75 (poly-phenolic oxidation) that allows organic matter breakdown in this environment
76 (Freeman et al. 2001). Plant community composition has been linked to soil phenol oxidase
77 activity in a temperate plant community (Kardol et al. 2010) and in principle similar drivers

78 may modulate phenol oxidase activity in Arctic plant communities. Generally, such
79 relationships have not been widely tested in Arctic ecosystems, apart from a study by Zak and
80 Kling (2006) who examined variations in phenol oxidase activity at the community-level,
81 together with a suite of extracellular enzymes, across a range of tundra communities.

82

83 To enable this assessment, we measured phenol oxidase activity, soil respiration rates
84 and mobile (water soluble) litter chemistry in a plant community with four co-existing
85 ericaceous shrub species. Our aims were firstly, to investigate the influence of plant species
86 cover on phenol oxidase activity in this plant community (according to relative spatial
87 differences in plant community composition), and secondly, to determine whether an
88 anticipated moth larval outbreak (in 2012) affected phenol oxidase activity, and related
89 parameters of litter biochemistry and C dynamics. We also sought to determine if responses
90 to the moth outbreak varied in patches dominated by different species in this community. We
91 firstly hypothesised that phenol-oxidase activity would be modulated by plant community
92 composition, because spatial differences in litter type and root activity would occur with
93 transitions in species abundance (at a patch-scale). The moth larval outbreak in the preceding
94 year was expected to reduce phenol oxidase activity because frass (insect waste) may return
95 mobile phenolics and nitrogen compounds to soil (Barbehenn and Martin 1992; Frost and
96 Hunter 2004), and nitrogen enrichment of highly lignified organic material is considered to
97 inhibit the production of phenol oxidase and result in highly-recalcitrant compounds that
98 resist decomposition (Hobbie 2008). Additionally, any precipitation washed through the
99 damaged vegetation canopy would input further nutrients and phenolics from exposed foliar
100 tissues (Tukey & Morgan 1963). In combination, therefore, these biochemical inputs from
101 herbivory were expected to drive negative relationships between larval herbivory and phenol
102 oxidase activity, due to aforementioned impacts from nitrogen (via increased levels of mobile

103 NH_4^+ in litter) and the influence of higher molecular weight phenolics in litter, including
104 condensed tannins, that may inhibit phenol oxidase activity (Allison, 2006). By contrast, soil
105 respiration rates were expected to be increased by herbivory, given an expected positive
106 effect of enriched biochemical inputs reaching the decomposer microbial community,
107 resulting in greater microbial activity.

108

109 **Materials and methods**

110 *Experimental site and location*

111 We sampled litter and soils from a 25 x 25m designated experimental study area of sub-
112 Arctic birch heath, 60m due north of the Abisko Research Station in northern Sweden (68.35
113 °N, 18.82°E) (Fig. 1). The study area lies at the interface between Arctic-boreal and tundra
114 biomes. The vegetation is sub-arctic *Empetrum-Vaccinium myrtillus* dwarf shrub heath, as
115 described by Sonesson and Lundberg (1974) and Oksanen and Virtanen (1995), comprising a
116 mosaic of ericaceous shrub vegetation largely dominated by *Empetrum hermaphroditum* L.
117 (quadrat cover range 0-61%, mean cover $18\% \pm 3.5$), with discrete highly abundant patches
118 of *Vaccinium myrtillus* L. (0-44%, $6.9\% \pm 2.1$), *V. vitis-idaea* L. (0-62%, $11.2\% \pm 2.9$), or *V.*
119 *uliginosum* L. (0-55%, 7.9 ± 2.5) (figures in parentheses are taken from our 2011 survey of
120 the experimental area). The soils in the area comprise a 2-20cm deep layer of highly organic
121 material ('O-horizon'), overlying glacial till interspersed by occasional erratics. This shallow
122 soil at the experimental site thaws completely to the mineral layer during summer and
123 maintains a stable temperature of $\sim 7^\circ\text{C}$ during July-August (*pers. obs.* A. Jones). Mean
124 monthly precipitation levels during July-August are 59.2 mm. Our investigations were
125 conducted during two summer growing seasons (July 2011 and July 2012). Extracellular
126 enzyme activities can vary greatly with season, being most inconsistent around the spring
127 thaw (Jefferies et al. 2010), hence, the detectability of enzymatic signals (e.g. from long-term

128 climate change drivers) in spring may be unfeasible due to sudden nutrient release from
129 thawing soils and litter (Henry 2012). By contrast, litter activities in frozen winter soils or
130 litters are also difficult to measure. Oxidising enzyme activities in Arctic soils have been
131 found to peak during summer (June-July) and decline during the late-summer early-autumn
132 senescence period (August-September) (Wallenstein et al. 2009, Sistla & Schimel 2013). We
133 chose to sample in summer (July) because phenol oxidase activities would be consistent and
134 active, and therefore functionally testable against our chosen (biotic) drivers.

135

136 In 2011, we investigated the influence of plant species cover on soil and litter phenol oxidase
137 activity. In 2012, a naturally recurring episodic outbreak of autumnal moth larvae (*Epirrita*
138 *autumnata* Borkhausen) was used to investigate how herbivory modulated litter phenol
139 oxidase activity, mobile litter NH_4^+ and phenolics, and soil respiration rates, as driven by
140 differences in plant community composition.

141

142 *Plant community composition and soil phenol oxidase activity*

143 Samples for the species composition study (22 July 2011) were taken using a micro corer
144 (10mm diameter) and a composite approach, whereby multiple sub-samples were combined
145 and homogenised for each sample point. Soil and litter samples were obtained from the 25 x
146 25m experimental area, at the intersections of regular grid co-ordinates. The experimental
147 vegetation area used had a flat aspect, low density birch canopy and a continuous understorey
148 shrub community. Hence, it was relatively homogeneous, apart from differences in shrub
149 community abundance at a patch scale. The shrub understorey in this habitat is a species
150 mosaic where discrete patches ($\sim 0.1\text{-}0.5 \text{ m}^2$) of the four main species dominate and between
151 these, a continuum of relative changes in community abundance is evident. Sampling in the
152 2011 assessment took place at 32 grid intersections (soil and litter) using 5m grid spacing (for

153 further information on the sampling grid arrangement see Online Resource 1). At each
154 sampling point, a 16 x 16 cm grid quadrat frame defined the collection area for litter and/or
155 soil. A 10 mm diameter corer (for soils) was used to obtain samples at 0-5 cm depth
156 (extracting approximately ~100g of material from 15 sub-sample cores, which were
157 combined and homogenised for each sampling point). Samples from the matrix of litter
158 suspended between the shrub canopy and the soil (i.e. 'shrub understorey' litter) were hand
159 collected. This litter layer is characteristic of many undisturbed heathland habitats, being an
160 unconsolidated mix of decaying plant material punctuated by fine roots and hyphae. Because
161 roots and fungal components were present, enzyme activities in litter reflected the combined
162 influence of both exudates from the microbial community and plant roots. Our 2012
163 assessment of larval impacts, therefore, focused only on the litter layer because it was
164 expected this would receive waste products immediately subsequent to larval herbivory. The
165 grid quadrat frame was also used to record vegetation data at sampling points, with cover
166 estimated by recording the presence or absence of each species in the 64 grid squares (2 cm x
167 2 cm).

168

169 *Insect outbreak assessment, litter sampling and soil respiration*

170 Starting in June 2012, the birch heath area surrounding Abisko Scientific Research Station
171 was subject to a naturally occurring episodic outbreak of autumn moth larvae (*Epirrita*
172 *autumnata*). The last larval outbreak occurred in 2004 (Morin 2013) and these events have a
173 return interval of ~9 years (Tenow 1972). The larval outbreak of 2012 was therefore
174 anticipated and we exploited this timing to assess how larval impacts further affected phenol
175 oxidase activity and soil surface respiration across this plant community using the same
176 experimental area as 2011. During the peak growing season of 2011 no larvae were found in
177 our experimental vegetation, hence, the impacts of herbivory for 2012 relate to larval foliar

178 damage in that year only. In our initial evaluations for 2012, the highest larval densities were
179 recorded on 12 July when local mean data showed $266.7 (\pm 60.6 \text{ s.e.})$ individuals m^{-2} ($n=10$,
180 0.03 m^2 sample area) in the shrub vegetation. Larval numbers gradually declined after this
181 time point. Occasional periods of rainfall (a mean of 6.4 mm per day during 12-23 July,
182 Abisko Scientific Research Station, *pers. comm.*) will have mobilised the soluble products of
183 larval waste following the outbreak (frass, greenfall and throughfall inputs leached from
184 damaged tissues) into litter and soil. Litter samples for the moth outbreak study were
185 collected on the 23 July 2012, (10 days after peak recorded larval density) when larval
186 numbers had largely subsided ($12.1 \text{ m}^{-2} \pm 1.5 \text{ s.e.}$) and when herbivore waste products were
187 expected to have been transferred to the litter, thereby, potentially impacting phenol oxidase
188 activity.

189

190 Material in 2012 was collected at 80 points, using a similar intersecting grid co-ordinates
191 approach as 2011 (Online resource 1), with a smaller grid spacing (3.1m) to provide a larger
192 number of sample points. Discrete dominant patches for each of the shrub species were used
193 for the 2012 study, allowing us to specifically target larval damage relationships for
194 individual species, in contrast to the gradual transitions in species abundance across this plant
195 community tested in 2011. In study on phenol oxidase activity in a temperate grassland
196 community, Kardol et al. (2010) used a similar sampling rationale to target individual plant
197 species. Because evergreen and deciduous species have differing shoot morphologies, shoot
198 damage from larval herbivory was defined separately for these distinct plant functional types.
199 The leading shoots at the tip of each branch (henceforth: ‘shoots’) from each species were
200 examined. The evergreen species (*E. hermaphroditum* and *V. vitis-idaea*) were recorded as
201 ‘damaged’ if the cuticle of the leading shoot had been consumed, leading to shoot tissue
202 browning. Shoots from the broad-leaved deciduous species (*V. myrtillus* and *V. uliginosum*)

203 were ‘damaged’ when >25% of the leaf material from any one shoot had been affected. This
204 distinction was used for deciduous species because if their shoots sustained <25% damage,
205 all leaves were typically retained, whereas greater levels of damage always incurred complete
206 loss of all leaves from the affected shoot tip.

207

208 We randomly assigned, *a priori*, one of the four shrub species as a ‘target’ for each of the 80
209 intersecting grid points ($n = 20$ per species) and at each of these points used the nearest patch
210 dominated by this species. In each case the sample points were <30cm from the grid
211 intersection and where the target species exceeded 50% of the total vegetation cover within a
212 16x16cm quadrat area (visually assessed using the presence or absence of shoots in 2x2cm
213 grid squares within the quadrat as a reference). The remaining two or three other species were
214 <50% cover in each case and, hence, could be considered ‘sub-dominant’ for that patch.

215 Damage scores for the dominant species in each patch were recorded by counting the
216 proportion of damaged shoots (damaged shoots / total shoots) within the 16 x 16cm quadrat
217 area (25.6 dm²) and litter was collected by hand from this area. Our area-based shoot
218 assessment method also accounted for the shoot density (shoots dm⁻²) of the dominant species
219 within the quadrat area (25.6 dm²) and was a measure of relative species abundance not
220 affected by foliar damage. By contrast, assessment methods for vegetation cover using
221 vegetation area would be affected by foliar damage. Although shoot damage varied greatly at
222 a patch scale (between 1 and 100% shoot damage was recorded for all sample points) an
223 assessment of shoot damage across all samples determined that the range of damage for each
224 species was spatially consistent across the experimental vegetation area. The potential for the
225 confounding effect of higher shoot densities to have facilitated greater amounts of shoot
226 damage was also investigated by regression, which was unable to show a relationship.

227

228

229 *In situ* litter-soil respiration rates were measured across the experimental vegetation
230 area on 5th August 2012 (~21 days after peak insect activity) to determine whether herbivore
231 activity had affected soil surface respiration rates. Respiration rates were measured using a
232 custom made (30mm diameter x 110mm long) PVC soil respiration chamber, fitted to an
233 infra-red gas analyser (IRGA) (EGM-3, PP-systems, Hitchin, UK). This respiration chamber
234 was held to the soil surface at the centre of a vegetation quadrat by opening the shrub canopy
235 and parting all stems to obtain an unvegetated area of litter and soil (henceforth simply,
236 ‘soil’) below. Pushing firmly on to undisturbed litter material at the soil surface created an
237 air-tight seal. Soil respiration rates, therefore, included a component of plant root respiration.
238 The CO₂-flux (change in CO₂ concentration sec⁻¹ cm⁻²) was calculated using internal IRGA
239 regression algorithms following gas exchange measurement for 120 seconds. A digital
240 thermometer (Cat number 36-1833, Clas Ohlson, Sweden) was used to record soil
241 temperature at the time of measurement. The sampling protocol for soil respiration rate
242 measurement followed a similar spatial (grid) arrangement to that used for litter collection.
243 Vegetation measurements of shoot density and shoot damage for the dominant species were
244 obtained at the time of respiration measurement using shoot counts and a 16 x16cm quadrat
245 frame. Two species were targeted for soil respiration assessment (*E. hermaphroditum* ($n=22$)
246 and *V. myrtillus* ($n=22$)) as, they were the most highly damaged evergreen or deciduous
247 species, despite *V. myrtillus* being of low overall abundance in this plant community. Soil
248 respiration data were collected at 44 intersecting grid points using a wider grid spacing
249 (4.2m) than the 2012 phenol oxidase survey because of the smaller total number of samples
250 taken in this aspect of the study, as only two species were sampled (Online resource 1).
251 However, the number of replicates per species ($n=22$) was higher than the 2012 phenol
252 oxidase assessment ($n=20$ per species) because the soil respiration chamber sampled a

253 smaller area (7.1cm²) than the 16 x 16 cm quadrat used in the phenol oxidase assessment. .
254 Similar to the above protocol, the most highly abundant (henceforth: ‘dominant’) target
255 species at each vegetation patch (where >50-90% of the total vegetation cover comprised a
256 dominant target species) was determined by prior random allocation for each intersection
257 point. The dominant patches (16 x 16 cm quadrat area) were always obtained < 30cms from
258 the grid intersection..

259

260 *Litter and soil sample processing*

261 Material collected from the 2011 species composition study comprised the litter layer
262 and O-horizon soil. In 2012, our assessment of larval outbreak impacts used litter only. In the
263 2011 study, soil samples were physically screened by soil layer dissection, so that only the
264 upper ‘organic-rich’ O-horizon layer was used. The depth of this soil layer varied between
265 locations, so a set soil depth could not be used to partition soil layers. Separation of the O-
266 horizon ensured that only the most active near-surface layer (usually a 0-2cm section depth)
267 of soil was used for analysis, being clearly identifiable from its high organic content. Any
268 visible roots from O-horizon soils or litter samples were removed by hand before further
269 processing. Given the highly organic nature of soil samples taken from a shallow-depth in
270 this habitat, no stones were present. Composite soil samples from a single sample point
271 (~100g) were homogenised in a laboratory bench top blender (Janke and Kunkel IKA
272 Labourtechnik, Germany), as were litter samples (~50g), at full power for 90 seconds until
273 the assay material developed a consistent coarse-ground state (<2 mm particle size). Samples
274 were either transferred immediately to the Abisko Scientific Research Station laboratory for
275 processing, or stored in a controlled temperature room at 5 °C.

276

277 *Laboratory analysis of soil and litter samples*

278 Soil and litter pH was measured from a 2:1 suspension in distilled water, following the
279 standard methodology of Allen et al. (1974). The percentage field moisture of each sample
280 was obtained by drying ~ 20g of the material at 80°C for 24 hrs and re-weighing. Analyses of
281 moisture content enabled assays on material at field moisture (phenol-oxidase activity,
282 mobile NH_4^+ and phenolics) to be expressed according to ‘equivalent dry weight’ and the
283 moisture data were further used as co-variates for some statistical analyses. Phenol oxidase
284 activities were assayed using the method of Pind et al. (1994), with randomly selected
285 duplicate samples processed for procedural precision checking (at 10 % of the total number
286 of samples). These duplicates confirmed a precision of >90%. The previously homogenised
287 litter or soil samples at field moisture were mixed in a 1:9 (soil: water) solution with high-
288 purity filtered water using a vortex mixer for 30 seconds. 3ml of this solution was introduced
289 to 4.5ml of water and 7.5ml of 10 mM *l*-dopamine phenylalanine (L-DOPA). We elected not
290 to use a buffer for this reaction, given that buffers themselves may interfere with enzymatic
291 activity (German et al. 2011) and because we wanted to assess the relative phenol oxidase
292 potential at the native pH for each of our substrates. Furthermore, the pH range of all litter
293 and soil samples fell within 1.2 pH units (4.69-5.93 pH range for all samples in the study),
294 hence, relative pH differences were expected to have only a small influence on phenol
295 oxidase activity. To address the potential influence of pH, however, we used a statistical
296 constraining method (in statistical models with phenol oxidase activity - see further details
297 under ‘Statistical analyses’). Phenol oxidase transforms an introduced colourless organic
298 phenol source, L-DOPA, to the red pigment 2-carboxy-2,3,-dihydroindole-5,6-quinone
299 (dicq), with the concentration measured by absorbance from a centrifuged aliquot using
300 spectrophotometry at 460 nm (Thermo Electron Corp., UK), following nine minutes
301 incubation at an ambient laboratory temperature of 20°C. The molarity of the final solution
302 was calculated according to a constant given by the Beer-Lambert law and the path-length of

303 the spectrophotometric cuvette (10mm) (Pind et al. 1994). Phenol oxidase activity was,
304 therefore, expressed as $\mu\text{Mol dicq (2,3-dihydroindole-5,6-quinone-2-carboxyate) g}^{-1}$ dry
305 weight min^{-1} , typically shortened to $\mu\text{Mol dicq g dry wt}^{-1} \text{min}^{-1}$. All sample readings were
306 obtained by first zeroing the spectrophotometer with an unreactive paired soil or litter sample,
307 which was prepared identically, but with distilled water replacing the L-DOPA. All paired
308 zero-corrected sample readings were zeroed from the absorbance of a sample containing only
309 10 mM L-DOPA and the relevant quantity of water. Organic matter content (2011 samples)
310 was determined in soils and litter by measuring weight loss on sample combustion to ash at
311 400 °C for 8 hrs (Allen et al. 1974). This analysis was not repeated on the 2012 litter samples,
312 because the 2011 litter samples consisted largely of organic matter (82-99%) and small
313 differences in this value were not statistically useful for interpreting the results in litter. Water
314 soluble (mobile) NH_4^+ and phenolics were extracted from 2012 litter samples using distilled
315 water following a similar procedure to Allen et al. (1974) for plant-available extraction. $3 \pm$
316 0.1 g litter at field moisture was suspended in 25ml water, shaken for one hour and filtered.
317 The extracts were analysed for total NH_4^+ concentration by automated UV-visible
318 colourimetry (Auto Analyzer III, Bran Luebbe, Chicago, IL) and total phenolic concentration
319 (expressed nominally as gallic acid equivalent) was determined by the Folin–Ciocalteu
320 method (Singleton et al. 1999), with solution absorbance measured via UV-visible
321 spectrophotometry (Biomate 5, Thermo-Electron Corporation, Woburn, MA).

322

323 *Statistical analyses*

324 Data analysis was performed using *R* v2.12.2 (*R* development core team 2011). The data were
325 analysed using generalised linear models (GLM), or generalised linear mixed effects models
326 (GLMM). In general, our analyses tested the relationship of a primary continuous factor
327 (percentage damaged shoots, species cover, or shoot density) on enzyme activities, mobile

328 NH_4^+ and phenolics and/or, soil respiration rate. Physiochemical substrate variables (organic
329 matter content, or moisture content) were also included as interacting co-variates in models to
330 test whether these contributed to relationships with phenol oxidase activity. These substrate
331 co-variates were specifically selected because they have been identified as important controls
332 on phenol-oxidase activity (Sinsabaugh 2008). In the case of phenol oxidase activities,
333 substrate pH was introduced as a ‘random effect’ using a mixed effects model (GLMM),
334 which statistically constrained the potential influence of pH on the ‘fixed effect’, phenol
335 oxidase activity. The soil respiration analysis also initially used soil temperature as a model
336 co-variate, but this did not increase the descriptive power of any model according to changes
337 in the Akaike Information Criterion (AIC) (Crawley 2009), so was discarded.

338

339 Multiple co-variates were evaluated in candidate models, using hierarchical stepwise
340 methods which removed co-variates and checked for improvements in AIC values (Crawley
341 2009). All response variables and co-variates were transformed where necessary using
342 logarithmic, square-root, or arc-sin functions (only in the case of percentage data), to gain
343 homogeneity of variance. Improvements in data conformity were confirmed according to
344 changes in the residual deviance values in model outputs.

345

346 **Results**

347

348 *Plant community composition and phenol oxidase activity*

349 In the 2011 community composition study, *E. hermaphroditum* cover had a strongly positive
350 and significant relationship with phenol oxidase activity in the organic O-horizon soil ($F_{1,28} =$
351 26.1 $P < 0.001$) (Fig. 2) (Table 1). A significant relationship for this species, with minimal
352 AIC values (suggesting the strongest model), was also detected when organic matter content

353 was included as a co-variate, although the significance of this model was less ($F_{1,28} = 4.6$ P
354 < 0.05); suggesting that, although the interaction with organic matter was significant, the co-
355 variate only weakly contributed to the statistical model. Litter phenol oxidase activity was not
356 significantly related to any variable in 2011, including *E. hermaphroditum* cover. No other
357 species cover relationships were significantly correlated, either with phenol oxidase activity,
358 organic matter content, substrate pH or substrate moisture content (some non-significant
359 model outputs are not shown in Table 1 for brevity). The soil and litter samples had a
360 consistently acidic pH range, and relatively high organic matter and moisture content (mean
361 values for these variables are given in Table 2).

362

363 *Insect outbreak relationships with phenol oxidase activity, mobile NH_4^+ and*
364 *phenolics, and soil respiration*

365 With the 2012 moth outbreak, damage by larvae occurred to varying degrees in all shrub
366 species. The data were not directly comparable between deciduous and evergreen species, as
367 different definitions of foliar ‘damage’ were used to account for differences between these
368 morphologically distinct plant functional types. Damage scores from either the two evergreen
369 species or the two deciduous species may be compared, however (Table 3). Of the evergreen
370 species, *E. hermaphroditum* had a greater mean level of damage ($55.1 \pm 9.4\%$ mean damage
371 score) than evergreen *V. vitis-idaea* ($37.6 \pm 7.8\%$ mean damage score), although the
372 difference between these species was non-significant ($P = 0.16$). Of the deciduous species, the
373 mean damage levels for *V. myrtillus* ($52.4 \pm 9.3\%$ mean damage score) and *V. uliginosum*
374 ($47.3 \pm 9.9\%$ mean damage score) were similar ($P = 0.71$). In *V. myrtillus* patches, a
375 significant negative relationship was detected between phenol oxidase activity and larval
376 damage ($F_{1,18} = 9.59$ $P < 0.01$) (Fig. 3). Phenol oxidase activity in the litter beneath *E.*
377 *hermaphroditum*, *V. vitis-idaea* and *V. uliginosum* had no relationship with the level of larval

378 damage (Table 4, 5), suggesting larval damage had not affected rates of phenol oxidase
379 activity in the litter of these species at the time of sampling. However, in *V. uliginosum* litter
380 larval damage had a strongly negative relationship with mobile NH_4^+ and phenolics (Table 5)
381 and in *V. vitis-idaea* litter, a weak negative relationship with mobile NH_4^+ (Table 4) that was
382 non-significant ($F_{1,18} = 3.59$ $P = 0.07$). Collectively, these results suggest herbivory reduced
383 the availability of NH_4^+ and/or mobile phenolics in the litter of these two *Vaccinium* species
384 at the time of sampling. In a similar direction to the soil phenol oxidase relationship with
385 cover found in 2011, *E. hermaphroditum* shoot density also had a strongly significant
386 positive relationship with soil respiration rates ($F_{1,20} = 12.2$ $P < 0.01$) (Fig. 4, Table 5) not
387 seen in *V. myrtillus*. Soil respiration rates were not significantly affected by the level of larval
388 damage under *E. hermaphroditum* or *V. myrtillus*.

389

390 **Discussion**

391

392 We firstly aimed to determine which plant species had the strongest influence on phenol
393 oxidase activity in this plant community, evidencing a positive relationship between *E.*
394 *hermaphroditum* abundance and phenol oxidase activity in shallow O-horizon soil for 2011.
395 This suggests that, during the peak growing season of a non-outbreak year, soil phenolic
396 decomposition processes in this habitat are a function of plant community composition and
397 such processes are principally influenced by *E. hermaphroditum*, an abundant species in this
398 community. It has been asserted that plant community composition in the Arctic is coupled to
399 below-ground processes (Hobbie 1992; Cornelissen et al. 2001; Dorrepaal et al. 2007) and by
400 finding relationships with the abundance of one species, our findings partly support this.
401 Additive effects from other shrub species in the community may have enhanced the phenol
402 oxidase relationship evident for *E. hermaphroditum* meaning that, more generally,

403 differences in community composition may contribute. Such additive effects may have
404 partially confounded this aspect of the analysis. Specific relationships between plant species
405 composition and phenol oxidase activity have been found in earlier studies on temperate
406 forests (Kourtev et al. 2003; Ushio et al. 2010), although no association has been investigated
407 previously for Arctic ecosystems. In a similar area of sub-Arctic heath to that in our study,
408 Hobbie (1996) showed that levels of polyphenolic lignin compounds in litter directly
409 influenced decomposition activity. Such an association may account for the positive phenol
410 oxidase relationship with *E. hermaphroditum* cover (Table 1). Measurement of soil
411 respiration rates after the larval outbreak of 2012 also showed a positive relationship with *E.*
412 *hermaphroditum* abundance (shoot density) (Table 6), indicating that increased litter-soil
413 biological activity is associated with this species during the peak growing season. In
414 combination, soil respiration and phenol oxidase relationships over two peak growing seasons
415 suggest an elevated level of biotic (root- and microbial) decomposition activity associated
416 with this species. This may be a characteristic feature of *Empetrum* dominated soils, roots and
417 their associated organic material, suggesting adaptations that facilitate localised control of
418 nutrient cycling and enhance the competitiveness of this species. This supports similar
419 conclusions made by Tybirk et al. (2000) in a synthesis of related *Empetrum* research,
420 pointing an allelopathic phenolic compound, batatasin-III present in litter that may also
421 inform high rates of phenol oxidase activity in the present study.

422

423 Our second aim was to determine whether a moth larval outbreak (in 2012) affected
424 litter decomposition processes over an acute timescale during the peak growing season. To
425 achieve this we sampled ~10 and ~21 days after peak larval activity, evidencing some short-
426 term effects of herbivory on decomposition. These are indicators of probable impacts on
427 nutrient dynamics for some species, which may persist in this community, particularly given

428 the short growing season and the relative sensitivity of this habitat to disturbance. However,
429 we accept that with a limited sampling window, some uncertainty remains as to how
430 transitory the effects we evidence are, or whether longer term impacts would affect other
431 elements of litter-soil carbon or nutrient cycling (e.g. via changes to soil respiration rates due
432 to a reduction in root biomass). In our study phenol oxidase activity was employed as an
433 indicator of changing biological processes in decomposing plant litter (Caldwell, 2005,
434 Kardol et al. 2010) (i.e. a decomposition bioindicator) at the soil surface, following the larval
435 outbreak. Herbivore nutrient inputs were potentially the strongest immediate driver of
436 enzyme activities, owing to hypothesised biochemical disturbance caused by waste inputs to
437 the litter surface (Weedon et al. 2011). In our short-term study, however, only phenol oxidase
438 activity in *V. myrtillus* litter was significantly affected; becoming reduced with increased
439 level of herbivore damage. Soil respiration rates, mobile NH_4^+ , or the total mobile phenolic
440 concentration under *V. myrtillus* were unaffected, suggesting that herbivory impacts in the
441 short term were limited to only litter phenol oxidase activity and had not perturbed other
442 elements relating to root activity or microbial nutrient uptake under this species. We
443 hypothesised that enhanced mobility of insect waste inputs would drive such phenol oxidase
444 changes, but this is unlikely because increased availabilities of NH_4^+ or total phenolics were
445 not observed. It is possible that reduced levels of phenol oxidase activity may be accounted
446 for by a decline in root-mycorrhizal exudate productivity following above-ground larval
447 damage. Such above- below-ground linkages from herbivore damage have been previously
448 proposed (Bardgett and Wardle 2003). Lower levels of phenol oxidase activity, therefore,
449 evidence a potential constraint on *V. myrtillus* to mobilise nutrients from litter during the
450 growing season, following foliar damage from larval outbreaks. By contrast, the significant
451 negative relationships in *V. uliginosum* litter between mobile NH_4^+ or total phenolic
452 compounds and larval damage, indicates immobilisation, or enhanced loss by leaching from

453 the litter layer, following herbivory. In this instance a negative relationship for mobile
454 compounds also contradicts our hypothesis. It is possible that some biochemical
455 immobilisation may have occurred due to complexation of NH_4^+ by polyphenolic tannin
456 compounds (Gundale et al. 2010), produced by *V. uliginosum* in response to herbivory.
457 However, such an explanation would not account for the reduction in mobile litter phenolics
458 also observed. NH_4^+ and other available compounds in larval waste may have been
459 biologically immobilised by ‘priming’ activity in the litter microbial-mycorrhizal community
460 (Lovett et al. 2002). Such an effect would stimulate luxury microbial consumption and,
461 therefore, immobilisation of mobile nutrients (Shen et al. 1984), between the start of the
462 outbreak and the time of sampling. Low-N adapted microbial communities are considered
463 highly competitive for recently mobilised mineral N (Kaye & Hart, 1997) and their foraging
464 ericaceous mycorrhizae can respond rapidly to new additions of mobile organically-bound
465 nutrients (Bajwa et al. 1985; Bending & Read 1995). Thus enhanced microbial nutrient
466 immobilisation under *V. uliginosum* is plausible and may explain the reduced mobility of
467 NH_4^+ seen in the litter of this species after larval herbivory. The lack of an equivalent
468 response in *V. myrtillus* may be accounted for by structural differences in the leaves of these
469 two species. *V. uliginosum* typically has greater levels of cell wall-bound phenolics and is
470 closer in leaf structure to evergreen *V. vitis-idaea*, whereas *V. myrtillus* leaves contain greater
471 levels of intra-cellular phenolics (Semerdjieva et al. 2003). Such differences would influence
472 transfer of these waste products to litter, because as higher molecular-weight phenolics are
473 less digestible for moth larvae (Barbehenn and Martin 1992).

474

475 Previously, soil enzyme research has focussed on abiotic drivers, including warming
476 and elevated nitrogen deposition, in disrupting enzyme activity in Arctic soils (Nemergut et
477 al. 2008; Sinsabaugh et al. 2008). Our study indicates that indirect changes via alterations in

478 plant community composition or the frequency of larval herbivory could be important drivers
479 of soil enzyme activity for this region. Because relationships differed between species, our
480 findings support the view that localised control over nutrient cycling is a key trait for Arctic
481 plants such as *Empetrum* (Hobbie 1992; Wookey et al. 2009). Herbivory has been highlighted
482 as an important and previously overlooked disturbance factor for boreal-tundra plant
483 communities at risk from future global change scenarios (Olofsson et al. 2009) and we
484 suggest that biotic interactions such as these, will affect litter and soil decomposition
485 processes differently across related communities according to local variations in community
486 composition. Decomposition processes under *E. hermaphroditum* appear relatively
487 unaffected by moth larval herbivory, however, evidence from our study suggests that
488 decomposition processes and litter nutrient dynamics under the more palatable deciduous
489 species; *V. myrtillus* and *V. uliginosum* are modified by herbivore impacts during the peak
490 growing season. As warmer climatic conditions perturb relationships between plants, soil and
491 primary consumers in the Arctic, the significance of such herbivore interactions with plant
492 community dynamics will intensify. It is important to consider these co-occurring influences
493 when evaluating climate-driven changes to Arctic ecosystems and their stores of organic C.

494

495

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686 change. *Glob Change Biol* 15: 1153-1172

687

688 Figure 1

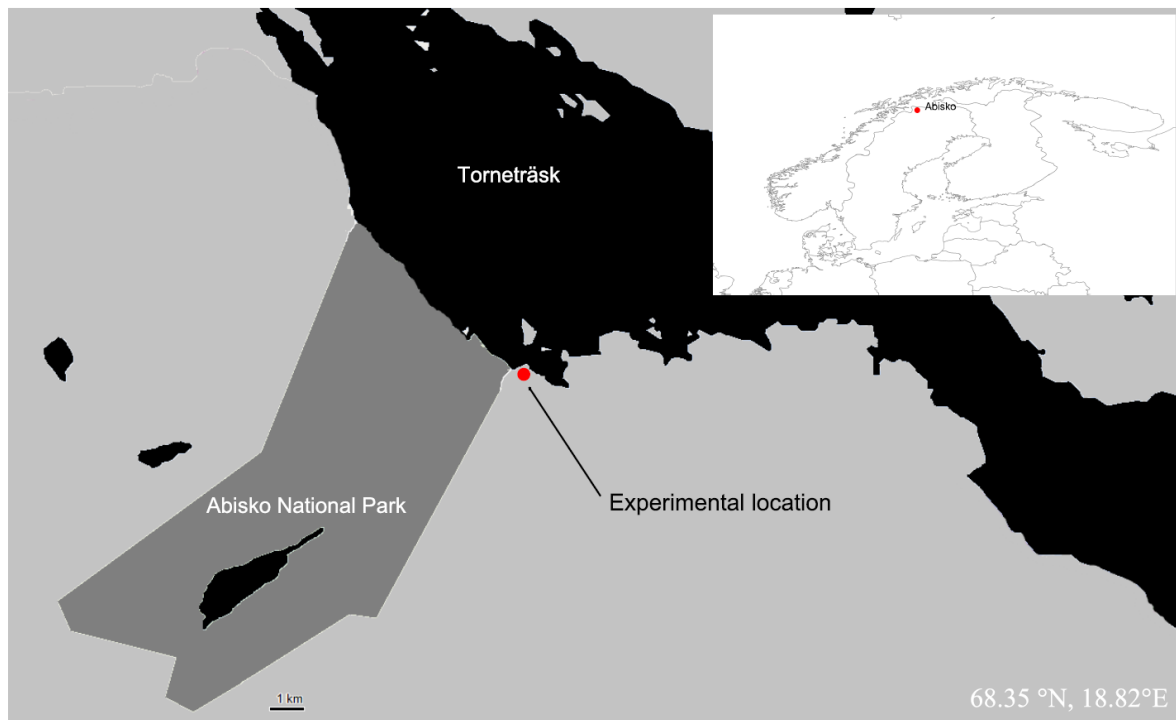


Figure 1: Map depicting location of experimental study area (indicated by circle), beside lake Torneträsk at the Abisko Research Station, northern Sweden (68.35 °N, 18.82°E).

689

690

Figure 2

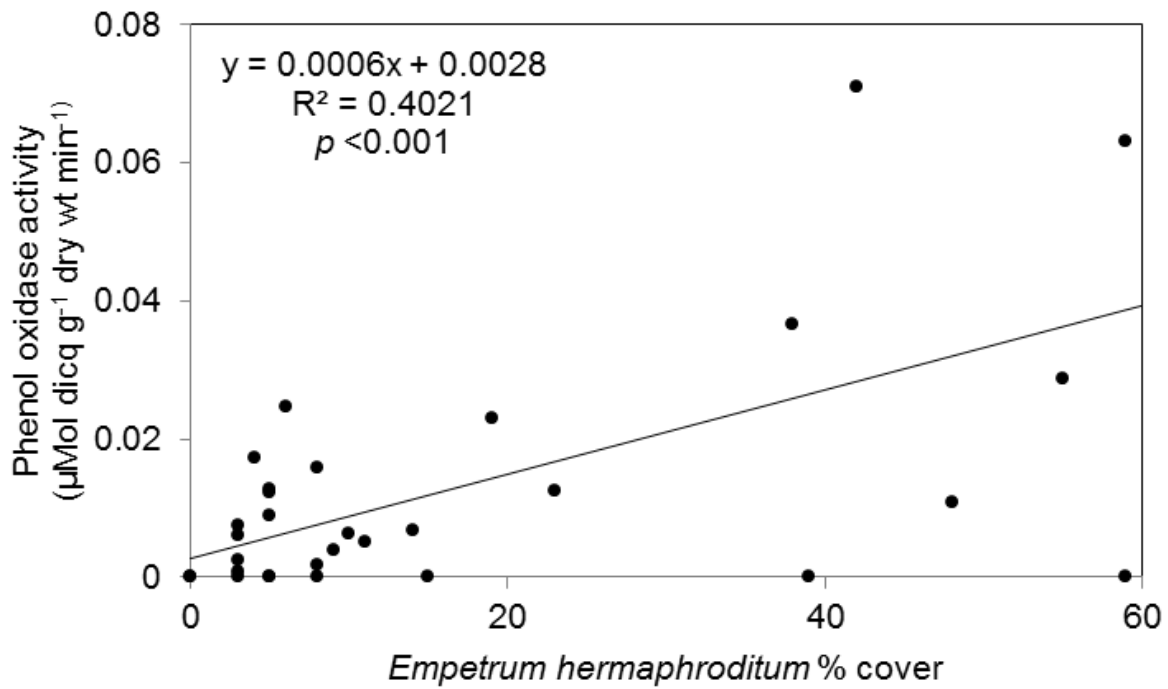
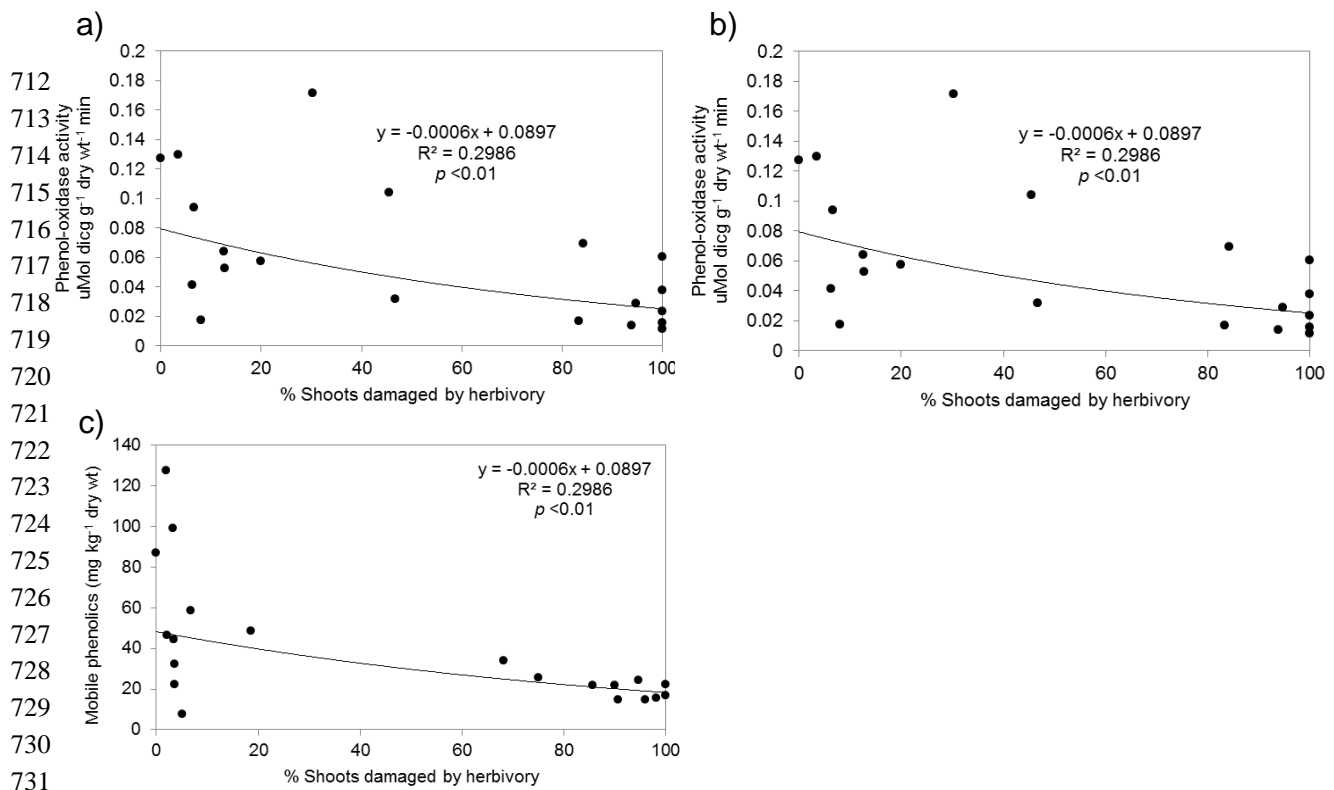


Figure 2: Scatterplot depicting the relationship between *E. hermaphroditum* percentage cover and O-horizon soil phenol oxidase activity. Regression line and R^2 value obtained on untransformed data by linear regression ($n=28$).

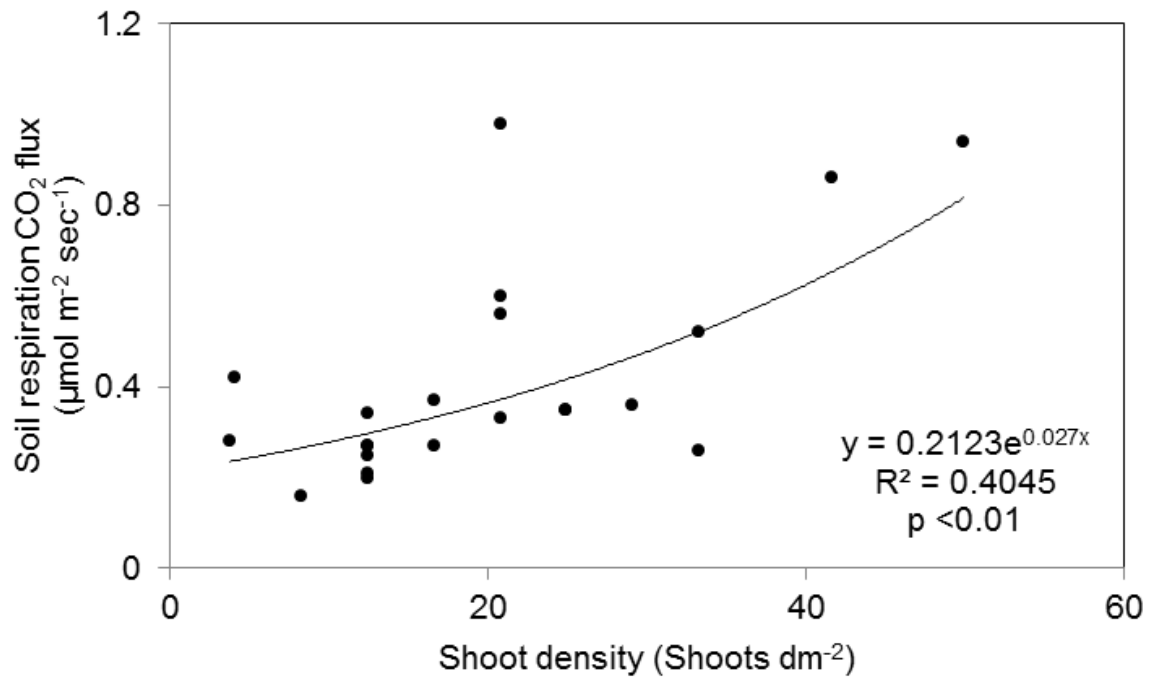
Figure 3



734 Figure 3: Scatterplot depicting the relationship between percentage shoot damage score and:
 735 a) *V. myrtillus* litter phenol oxidase activity, b) *V. uliginosum* litter mobile NH_4^+ , c) *V.*
 736 *uliginosum* mobile phenolics. Regression line equation and R^2 value as shown were obtained
 737 by regression with an exponential function fitted to values for percentage shoot damage score
 738 ($n=20$).

Figure 4

739



740

741

742 Figure 4: Scatterplot depicting the relationship between *Empetrum hermaphroditum* shoot
743 density score and soil respiration rate. Regression line equation and R² value as shown were
744 obtained by by regression with an exponential function fitted to values for shoot density
745 ($n=22$).

746

747

748

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750

751

752 **Table Legends**

753

754 Table 1: Statistical summary table for uni- or multivariate GLMM analyses of phenol-oxidase
 755 activity in 2011 for (Model 1) litter or (Model 2) O-horizon soil according to *Empetrum*
 756 *hermaphroditum* cover. For brevity, non-significant outputs for all modelled relationships
 757 with other species are not shown. Substrate moisture or organic matter were included as
 758 interacting variables (as fixed effects). Degrees of freedom for numerator and denominator
 759 (df_n , df_d), F and P values given. P values in the table are at * $P < 0.05$, *** $P < 0.001$ levels
 760 of statistical significance.

761

762 Table 2: Data summary, showing minimum, maximum and mean values for: pH, organic
 763 matter content moisture content, mobile NH_4^+ and mobile total phenolics in (1) 2011: mixed-
 764 species litter and O-horizon samples and (2) 2012: dominant species patches.

765

766 Table 3: Data and statistical summary of 2012 larval foliar damage scores per shrub species
 767 with outputs for GLM differences between non-deciduous and deciduous species. Maximum,
 768 minimum, and mean (\pm s.e.) percentage larval damage scores are grouped according to pairs
 769 of evergreen and deciduous species, measured 11 days after peak larval activity on the 23rd
 770 July 2012.

771

772 Table 4: Statistical summary table for uni- and multivariate GLMM analyses of 2012 phenol-
 773 oxidase activity, mobile NH_4^+ and mobile total phenolics in litter from patches dominated by
 774 evergreen *Empetrum hermaphroditum* and *V. vitis-idaea*, an deciduous *Vaccinium myrtillus*
 775 and *V. uliginosum*, showing relationships with herbivory damage (% damaged shoots) and
 776 shoot density (shoots dm^{-2}). Substrate and species composition variables were also tested in
 777 multi-variate analyses with phenol oxidase activity. Only model outputs with the strongest
 778 Akaike information criterion (AIC) value are presented for brevity. Degrees of freedom for
 779 numerator and denominator (df_n , df_d), F and P values in the table are at ** $P < 0.01$ level of
 780 statistical significance. AIC values were used for comparing contenting multi-variate models
 781 (these models are not shown for brevity). For a near-statistically significant model, the
 782 direction of the slope estimate (\pm) for the modelled relationship between the primary
 783 explanatory variable and phenol-oxidase activity is given.

784

785 Table 5: Statistical summary table showing univariate GLM analyses of 2012 soil respiration
 786 rates in litter from patches dominated by 2 of the dwarf-shrub species in the study, showing
 787 relationships with herbivory damage (% damaged shoots) and shoot density (shoots dm^{-2}).
 788 Degrees of freedom for numerator and denominator (df_n , df_d), F and P values given. P value
 789 in the table is at ** $P < 0.01$ levels of statistical significance. AIC values were used for
 790 comparing contenting multivariate models (these weaker models are not shown for brevity).
 791 For the statistically significant model, the direction of the slope estimate (\pm) for the modelled
 792 relationship between the primary explanatory variable and soil respiration rate is given.

Table 1

Comparison of species cover effects on phenol oxidase activity											
Model 1						Model 2					
Litter phenol oxidase	d.f. _d	d.f. _n	<i>F</i>	<i>P</i>	<i>AIC</i>	O-horizon phenol oxidase	d.f. _d	d.f. _n	<i>F</i>	<i>P</i>	<i>AIC</i>
<i>Empetrum hermaphroditum</i>											
Cover	28	1	3.2	0.08	-103.4	Cover	28	1	26.1	***	-146.7
Cover x moisture	24	1	0.1	0.79	-56.3	Cover x moisture	24		1.9	0.18	-111.2
Cover x organic matter	24	1	0.0	0.93	-66.1	Cover x organic matter	24	1	4.6	*	-116.7
Substrate variables											
Moisture	28	1	2.0	0.17	-93.7	Moisture	28	1	0.0	0.98	-131.7
Organic matter	28	1	1.3	0.26	-97.1	Organic matter	28	1	0.2	0.66	-133.1

794 Table 1: Statistical summary table for uni- or multivariate GLMM analyses of phenol-oxidase
795 activity in 2011 for (Model 1) litter or (Model 2) O-horizon soil according to *Empetrum*
796 *hermaphroditum* cover. For brevity, non-significant outputs for all modelled relationships
797 with other species are not shown. Substrate moisture or organic matter were included as
798 interacting variables (as fixed effects). Degrees of freedom for numerator and denominator
799 (df_n, df_d), *F* and *P* values given. *P* values in the table are at * *P* < 0.05, *** *P* < 0.001 levels
800 of statistical significance.

Table 2

Variable	Minimum	Maximum	Mean (\pm s.e.)
<i>Mixed species litter (2011)</i>			
pH	4.3	5.7	4.9 \pm 0.05
Organic matter content (%)	82.7	99.1	96.3 \pm 0.6
Moisture (%)	9.2	86.8	45.6 \pm 3.8
<i>Mixed species O-horizon soil (2011)</i>			
pH	4.1	5.9	4.7 \pm 0.07
Organic matter content (%)	74.5	99.1	94.8 \pm 0.9
Moisture (%)	39.1	77.4	59.6 \pm 1.6
<i>Empetrum hermaphroditum litter (2012)</i>			
pH	4.99	5.9	5.5 \pm 0.06
Moisture (%)	55.1	71.9	63.8 \pm 1.0
Mobile NH ₄ ⁺ (mg kg ⁻¹ dry wt)	5.6	285.8	59.3 \pm 17.1
Mobile phenolics (mg kg ⁻¹ dry wt)	27.9	189.9	69.6 \pm 8.7
<i>Vaccinium vitis-idaea litter (2012)</i>			
pH	4.9	5.8	5.5 \pm 0.06
Moisture (%)	32.1	73.8	56.7 \pm 2.2
Mobile NH ₄ ⁺ (mg kg ⁻¹ dry wt)	10.2	226.7	60.0 \pm 12.7
Mobile phenolics (mg kg ⁻¹ dry wt)	28.5	117.3	60.0 \pm 5.2
<i>V. uliginosum litter (2012)</i>			
pH	4.9	5.9	5.5 \pm 0.07
Moisture (%)	52.0	72.4	64.6 \pm 1.4
Mobile NH ₄ ⁺ (mg kg ⁻¹ dry wt)	11.6	270.1	66.1 \pm 14.9
Mobile phenolics (mg kg ⁻¹ dry wt)	7.8	127.8	39.3 \pm 7.1
<i>V. myrtillus litter (2012)</i>			
pH	4.9	5.8	5.4 \pm 0.06
Moisture (%)	38.7	65.3	53.9 \pm 1.7
Mobile NH ₄ ⁺ (mg kg ⁻¹ dry wt)	5.8	239.0	67.7 \pm 14.6
Mobile phenolics (mg kg ⁻¹ dry wt)	22.9	634.5	73.2 \pm 30.0

801 Table 2: Data summary, showing minimum, maximum and mean values for: pH, organic
802 matter content moisture content, mobile NH₄⁺ and mobile total phenolics in (1) 2011: mixed-
803 species litter and O-horizon samples and (2) 2012: dominant species patches.

Table 3

Species	Maximum (%)	Minimum (%)	Mean (% ± s.e.)	d.f. _d	<i>F</i>	<i>P</i>	<i>AIC</i>
<i>Empetrum hermaphroditum</i>	100	1.8	55.1 ± 9.4				
<i>Vaccinium vitis-idaea</i>	89.6	0	37.6 ± 7.8	38	2.04	0.16	41.7
<i>V. myrtillus</i>	100	0	52.4 ± 9.3				
<i>V. uliginosum</i>	100	0	47.3 ± 9.9	38	0.14	0.71	50.0

804 Table 3: Data and statistical summary of 2012 larval foliar damage scores per shrub species
805 with outputs for GLM differences between non-deciduous and deciduous species. Maximum,
806 minimum, and mean (\pm s.e.) percentage larval damage scores are grouped according to pairs
807 of evergreen and deciduous species, measured 11 days after peak larval activity on the 23rd
808 July 2012.
809

Table 4

Relationships in litter for evergreen species		<i>Slope</i>	d.f.	<i>F</i>	<i>P</i>	<i>AIC</i>
<i>Empetrum hermaphroditum</i>						
% Damaged shoots:	phenol oxidase activity		16	0.00	0.95	33.8
	Mobile NH ₄ ⁺		18	1.39	0.25	29.3
	Mobile total phenolics		18	2.50	0.13	28.1
Shoot density:	phenol oxidase activity		16	2.00	0.18	31.2
	Mobile NH ₄ ⁺		18	1.09	0.31	29.6
	Mobile total phenolics		18	0.80	0.38	29.4
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<i>Vaccinium vitis-idaea</i>						
% Damaged shoots:	phenol oxidase activity		16	0.31	0.59	27.8
	Mobile NH₄⁺	-	18	3.59	0.07	22.6
	Mobile total phenolics		18	0.51	0.49	27.6
Shoot density:	phenol oxidase activity		16	1.16	0.30	25.9
	Mobile NH ₄ ⁺		18	0.12	0.73	26.0
	Mobile total phenolics		18	2.47	0.13	20.4
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Relationships in litter for deciduous species						
<i>Vaccinium myrtillus</i>						
% Damaged shoots:	phenol oxidase activity	-	16	9.59	**	19.1
	Mobile NH ₄ ⁺		18	0.32	0.58	30.5
	Mobile total phenolics		18	0.52	0.41	29.8
Shoot density:	phenol oxidase activity		16	2.09	0.17	26.5
	Mobile NH ₄ ⁺		18	0.09	0.77	30.7
	Mobile total phenolics		18	2.51	0.13	28.2
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<i>V. uliginosum</i>						
% Damaged shoots:	phenol oxidase activity		16	1.27	0.28	39.6
	Mobile NH₄⁺	-	18	11.1	**	14.1
	Mobile total phenolics	-	18	10.2	**	39.4
Shoot density:	phenol oxidase activity		16	0.50	0.50	48.5
	Mobile NH ₄ ⁺		18	2.49	0.13	21.1
	Mobile total phenolics	+	18	3.11	0.09	45.2

838 Table 4: Statistical summary table for uni- and multivariate GLMM analyses of 2012 phenol-
839 oxidase activity, mobile NH₄⁺ and mobile total phenolics in litter from patches dominated by
840 evergreen *Empetrum hermaphroditum* and *V. vitis-idaea*, an deciduous *Vaccinium myrtillus*
841 and *V. uliginosum*, showing relationships with herbivory damage (% damaged shoots) and
842 shoot density (shoots dm⁻²). Substrate and species composition variables were also tested in
843 multi-variate analyses with phenol oxidase activity. Only model outputs with the strongest
844 Akaike information criterion (AIC) value are presented for brevity. Degrees of freedom for
845 numerator and denominator (df_n, df_d), *F* and *P* values in the table are at ** *P* < 0.01 level of
846 statistical significance. AIC values were used for comparing contenting multi-variate models
847 (these models are not shown for brevity). For a near-statistically significant model, the
848 direction of the slope estimate (±) for the modelled relationship between the primary
849 explanatory variable and phenol-oxidase activity is given.

850

Table 5

Relationships with soil respiration	Slope	d.f. _d	F	P	AIC _c
<i>Empetrum hermaphroditum</i>					
% Damaged shoots		20	1.80	0.19	3854
Shoot density	+	20	12.2	**	2655
<i>Vaccinium myrtillus</i>					
% Damaged shoots		20	1.2	0.29	1857
Shoot density		20	0.3	0.59	1858

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863 Table 5: Statistical summary table showing univariate GLM analyses of 2012 soil respiration
 864 rates in litter from patches dominated by two of the dwarf-shrub species in the study, showing
 865 relationships with herbivory damage (% damaged shoots) and shoot density (shoots dm⁻²).

866 Degrees of freedom for numerator and denominator (df_n, df_d), F and P values given. P value
 867 in the table is at ** P < 0.01 levels of statistical significance. AIC values were used for
 868 comparing contenting multivariate models (these weaker models are not shown for brevity).

869 For the statistically significant model, the direction of the slope estimate (±) for the modelled
 870 relationship between the primary explanatory variable and soil respiration rate is given.

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