**Title:** Tracking the fate of fresh carbon in the Arctic tundra: Will shrub expansion alter responses of soil organic matter to warming?

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**Abstract**

Rapid climate warming in the Arctic threatens to destabilize vast stocks of soil carbon (C) that have accumulated over millennia, which could amplify the C-climate feedback. However, climate-induced shrub expansion may counteract these losses if their higher-quality litter (lower C:N) is efficiently incorporated into microbial products and stabilized within the soil. Alternatively, increased C inputs could stimulate microbial decomposition of old soil organic matter (SOM) through priming mechanisms. We investigated whether inputs of low molecular weight carbon (LMW-C) induced SOM priming or retention in soils underlying *Eriophorum vaginatum*, an ubiquitous tussock-forming sedge, and *Betula nana,* a dominant shrub that is expanding its range and coverage across the Arctic. We did not find evidence of priming, defined as an increase in the decomposition of native SOM stocks, from soils underlying either vegetation type. However, microbial respiration of new LMW-C inputs was twice as high in soils underlying *E. vaginatum* than *B. nana,* while belowground retention of new LMW-C inputs was 150% higher in soils underlying *B. nana.* Our results highlight the extraordinary capacity of shrub-colonized soils to retain new C inputs belowground, which may mitigate soil C loss as the Arctic climate warms.

## 1. Introduction

The vulnerability of vast carbon (C) stocks stored in Arctic soils to rapid climate warming is widely recognized (Crowther et al., 2016; Mack et al., 2004). But, climate warming is also increasing plant productivity, which could either ameliorate or enhance soil C loss (Natali et al., 2012; Sistla et al., 2013). The potential for C inputs to balance losses will depend on how efficiently plant-derived C is incorporated into microbial products, the precursor of soil organic matter (SOM) formation, *versus* converted to $CO_2$ and released to the atmosphere (Cotrufo et al., 2013). In addition, new plant litter and root exudate inputs might enhance the decomposition of old SOM through a process known as priming (Fontaine et al., 2003; Kuzyakov, 2002). Thus, enhanced plant productivity in the Arctic could either promote the formation of new soil C, or increase losses of native soil C, making vegetation responses to warming a critical regulator of global C cycling.

The net effects of rapid climate change on Arctic soil C stocks are mixed, with evidence of massive greenhouse gas release to the atmosphere (Commane et al., 2017; Crowther et al., 2016; Mack et al., 2004; Schuur et al., 2008), as well as recovery of soil C stocks following perturbation (Jiang et al., 2015; Natali et al., 2012; Sistla et al., 2013). Several responses to warming will likely modulate the balance between C release and storage. Warmer winters (Christensen et al., 2013) are degrading permafrost and deepening active layer thaw depths (Hodgkins *et al.*, 2014; Liljedahl *et al.*, 2016), which could expose newly liberated C to rapid microbial metabolism (Mackelprang et al., 2011; Marín-

61 Spiotta et al., 2014). At the same time, lengthening growing seasons (Ernakovich et al.,
62 2014; Livensperger et al., 2016) have fundamentally altered vegetation composition and
63 productivity (Chapin et al., 1995; Deslippe and Simard, 2011; Sturm et al., 2001), the
64 effects of which are diffusing belowground (Hartley *et al.*, 2012). Specifically, greater
65 plant productivity is expected to increase the release of root exudates belowground
66 (Brüggemann et al., 2011), which are primarily composed of low molecular weight C
67 compounds (LMW-C) (Jones et al., 2009). These LMW-C compounds may stimulate
68 decomposition of native SOM (Hartley et al., 2012; Mack et al., 2004) by inducing a
69 positive priming effect to relieve microbial nutrient limitation (Kuzyakov, 2002). As a
70 result, greater extracellular enzyme production could increase nutrient mobilization from
71 native SOM and contribute to net soil C loss (Kuzyakov, 2010). Alternatively, new
72 LMW-C inputs could reduce SOM turnover if microbial substrate use efficiency (SUE)
73 increases and microbial products are stabilized through organo-mineral complexation
74 (Cotrufo et al., 2013; Kallenbach et al., 2016; Schmidt et al., 2011).
75
76 The influence of vegetation on belowground nutrient availability may influence the net
77 effect of LMW-C inputs on soil C stocks (Hartley et al., 2012). Widespread increases in
78 primary productivity have been attributed to rapid expansion of *Betula nana* shrubs
79 (Sturm et al., 2001). The success of these shrubs is facilitated by phenotypic traits that
80 allow them to outcompete other species, including *Eriophorum vaginatum,* a dominant
81 tussock-forming sedge (Bret-Harte et al., 2001; Chapin et al., 1995; Deslippe and Simard,
82 2011; Koyama et al., 2013; Shaver et al., 2001; Sistla et al., 2013). These traits include
83 developmental plasticity (Bret-Harte et al., 2001), formation of N-acquiring and C-

84 sharing ectomycorrhizal networks (Deslippe and Simard, 2011), and snow entrapment,
85 which facilitates over-winter SOM mineralization and release of nutrients for shrub
86 uptake the following spring (Schimel et al., 2004; Sturm et al., 2001). Associations
87 between *B. nana* and N-acquiring ectomycorrhizal networks increase shrub litter and soil
88 N concentrations (Deslippe and Simard, 2011) relative to non-mycorrhizal, N poorer, *E.*
89 *vaginatum* systems (Sullivan et al., 2007). The difference in N availability belowground
90 could increase the magnitude of priming resulting from new LMW-C inputs in *E.*
91 *vaginatum* soils, particularly during peak plant productivity when nutrient competition is
92 intensified (Zhu et al., 2016). Thus, cascading effects of *B. nana* expansion may release
93 microbial energetic and nutrient constraints relative to *E. vaginatum* soils, reducing the
94 magnitude of SOM priming.
95
96 To test the effect of LMW-C inputs on native soil C stocks, we applied $^{13}$C-enriched
97 glucose—a model root exudate (Dijkstra et al., 2011; Strickland et al., 2012)—to Arctic
98 tundra soils underlying *E. vaginatum* and *B. nana*. We used two-pool isotope mixing
99 models to track the proportion of LMW-C converted to $CO_2$, assimilated in microbial
100 biomass, transformed to dissolved organic matter, and retained in bulk soil. We captured
101 the influence of season on LMW-C fate by amending soils in July (peak biomass),
102 September (senescence), and May (spring thaw). To determine whether LMW-C
103 persisted longer-term, we measured responses 54 and 306 days following amendment.
104 We posit that the fate of LMW-C and the magnitude and direction of priming is driven by
105 SOM stoichiometry (e.g. C:N). With this rationale, we test three predictions: (1) LMW-C
106 input increases SOM turnover, with the largest priming effect—and lowest microbial

SUE—in higher C:N soils underlying *E. vaginatum*; (2) the magnitude of these effects vary seasonally and are negatively correlated with soil N concentrations; (3) the proportion of LMW-C retained belowground is positively correlated with microbial SUE.

*Figure 1*

## 2. Methods

### *2.1 Site description*

We established study plots in May 2014 in a moist acidic tundra site near Toolik Lake Field Station, Alaska, USA (68˚ 38'N, 149˚ 34'W). Mean annual temperature at Toolik Field Station is -8°C, with average summer temperatures near 10°C and average winter temperatures near -20°C (Hobbie and Kling, 2014). Mean annual precipitation is 318 mm, with 43% falling as snow (Schimel et al., 2004). The region is dominated by *Eriophorum vaginatum,* a tussock forming sedge, *Betula nana,* a dwarf birch, and mosses, which together comprise approximately 45% of above and belowground biomass (g $m^{-2}$) (Hobbie and Chapin, 1998). The soils are classified as Ruptic Histic Aquiturbels (Borden et al., 2010) and have an average pH of 4.9. Average soil C stocks in the top 20 cm were 2,150 ± 335 g C $m^{-2}$ in soils underlying *B. nana* and 2,282 ± 296 g C $m^{-2}$ in soils underlying *E. vaginatum.* We observed the deepest active layers at our plots in July 2014, averaging 10 cm beneath *B. nana* and >20 cm beneath *E. vaginatum.* Unfortunately, we did not measure species-specific soil temperatures, however previous research has shown

130 temperatures are similar between graminoid and shrub dominated communities (Bradley-
131 Cook et al., 2016). Thus, although areas colonized by dense, tall shrubs may increase
132 latent heat fluxes (McFadden, 1998) and could reduce temperatures relative to within-
133 tussock soils (Chapin III et al., 1979), these effects are not always propagated
134 belowground (Sturm et al., 2001).
135
136 We selected three time periods for our study that represent important seasonal stages in
137 the Arctic: peak productivity (July 24–August 6, 2014), senescence (September 6–
138 September 18, 2014), and thaw (May 19–May 30, 2015). Precipitation and temperature
139 data for each sampling period were acquired from the Toolik Long Term Ecological
140 Research database (Shaver and Laundre, 2010). Cumulative precipitation was 39.6 mm
141 during peak plant productivity, 2.0 mm during senescence, and 55.3 mm during thaw.
142 Mean soil temperatures at 5 cm depth were 9.1 (± 0.6) °C during peak plant productivity,
143 3.0 (± 0.5) °C during senescence, and 6.65 (± 0.3) °C during thaw. Average annual
144 precipitation and soil temperatures are reported for 2014, 2015, and the ten-year average
145 (2005-2015) in SI Table 1.
146
147 *2.2 Experimental design*
148
149 Our experiment consisted of three factors: vegetation type (*B. nana* or *E. vaginatum),*
150 LMW-C addition (amended or control), and month (July, September, or May). We
151 replicated each treatment four times in a fully randomized block design, where each 5x5
152 $m^2$ block was spaced 10 m apart. Our experimental unit was a PVC collar (10 cm

153 diameter and 15 cm tall), which we installed around a tussock or shrub plant, maintaining
154 a minimum spacing of 1 m between collars.
155
156 We installed 12 collars in each block (2 vegetation types * 2 additions * 3 months) in
157 May 2014 and let them equilibrate for 45 days before amending soils within treatment
158 collars with LMW-C. Soils were amended July 28, 2014, September 11, 2014, or May
159 22, 2015. We amended each collar with $^{13}$C-enriched (10 atom%) glucose solution at 640
160 μg C $g^{-1}$ soil. This corresponded to approximately 36 g glucose $m^{-2}$, assuming a 10 cm
161 organic horizon and a bulk density of 0.075 g $cm^{-3}$. The LMW-C addition increased
162 average soil C concentrations in the top 20 cm by 1.7%; we selected this relatively low
163 tracer concentration to avoid inducing a direct C fertilization effect and to minimize
164 impacts on ongoing metabolic processes (Dijkstra et al., 2011). To achieve even
165 distribution throughout the amended soil profile, we added 5 ml of substrate with a 20-
166 gauge needle (Becton Dickinson) at five equidistantly spaced points, continuously
167 injecting substrate from 5 cm depth to the soil surface.
168
169 Two additional collars were installed around *B. nana* and *E. vaginatum* plants in each
170 block allowing us to monitor the influence of elevated LMW-C availability on
171 intermediate and long-term Arctic C cycling. These collars were amended July 28, 2014
172 and harvested either 49 days (September 11, 2014) or 306 days (May 30, 2015) following
173 amendment. Control collars in each block remained undisturbed for the duration of the
174 experiment and were used as background end members in the two-pool isotope-mixing
175 model (see *Data Analysis*).

176

177 *2.3 $CO_2$ measurements*

178

179 LMW-C amended and control (non-amended) soils were measured in the field for $CO_2$
180 concentrations (ppm) and $^{13}CO_2$ enrichment (‰) using a Picarro G2101-*i* (Picarro Inc.,
181 Sunnyvale, CA, USA) portable cavity ring-down spectroscopy analyzer (CRDSA). The
182 CRDSA was frequently calibrated using high-purity $CO_2$ calibrant gas with a range of
183 $CO_2$ concentrations and isotopic values (Cambridge Isotope Laboratories CLM-3783-10;
184 Airgas UHP300). $CO_2$ concentrations and $^{13}C$- $CO_2$ isotope values were validated with a
185 Li-Cor LI 6252 Infrared gas analyzer (Li-Cor Inc., Lincoln, NE, USA) and a PreCon
186 Delta V IRMS coupled to a GC-isolink unit (Thermo Scientific, Waltham, MA, USA) at
187 Colorado State University.

188

189 To allow continuous flux measurements at our field site, we coupled the CRDSA to an
190 external recirculating vacuum pump and eliminated water interference using a
191 magnesium perchlorate water trap (<0.03% $H_2O$; Agilent Technologies MT120-4). We
192 used Bev-A-Line stainless steel flexible tubing (Swagelok 321-4-X-24DFR) to connect
193 the CRDSA to the water trap and recirculation pump, as well as to a 10 cm diameter PVC
194 cap fit with two 6.35 mm Swagelok stainless steel ports (SS-4-VCR-6-DM). The
195 connection of the PVC cap and collar formed a gas tight seal that was fitted with a foam
196 gasket (LiCor 8100-632).

197

198 $CO_2$ and $\delta^{13}C$-$CO_2$ was measured in the amended soils after six and twelve hours, and

199 one, three, five, seven, and ten days. Amended soils incubated for intermediate length
200 were measured again four times after approximately 1.5 months (43, 44, 48, 49 days) of
201 *in situ* incubation, and long-term soils were measured again after approximately 11
202 months (44, 50, 302, and 305 days) of *in situ* incubation. Control soils were measured for
203 $^{13}CO_2$ flux twelve times during the course of the study (five times in July, five times in
204 September, and two times in May). Corrections were applied to $CO_2$ effluxes using an
205 average hourly soil temperature at 5 cm depth to account for variability. We connected
206 the CRDSA to each collar for a sufficient period of time to allow an increase of at least
207 100 ppm $CO_2$ , and $^{-}$5‰ $\delta^{13}C$ for control soils and $^{+}$100‰ $\delta^{13}C$ for treatment soils. This
208 range of $CO_2$ concentration and isotope enrichment was sufficient to quantify the
209 exchange processes of $CO_2$ between terrestrial and atmospheric reservoirs and to apply
210 the Keeling plot method to estimate $^{13}C$ of the soil $CO_2$ efflux (Cotrufo et al., 2014;
211 Keeling, 1958; Köhler et al., 2006). We calculated the $^{13}C$-$CO_2$ signature as the y-
212 intercept of the linear regression of $^{13}C$ versus the inverse $CO_2$ concentration ($r^2 \geq 0.98$).
213 We flushed the CRDSA with ambient air between measurements and began subsequent
214 measurements after $CO_2$ concentrations and isotope enrichment returned to background
215 levels.
216
217 *2.4 Soil collection and processing*
218
219 At each harvest date (July 29, 2014, September 21, or May 31, 2015) we collected
220 control and LMW-C amended soils by cutting around the PVC collar with an ethanol-
221 sterilized, serrated knife. We split soil cores into a surface sample (0-10 cm) and a

222 subsurface sample (10-20 cm), which roughly corresponded to the organic and mineral
223 horizon (± 5.3 cm). Each sample was bagged individually and shipped frozen to Colorado
224 State University for analysis, where they were stored until processing. In the laboratory,
225 green litter and live roots were removed and samples were thoroughly homogenized by
226 hand. Soils were sub-sampled for gravimetric water content, C and N elemental and
227 isotopic analyses, extractable nutrients, microbial biomass, and potential extracellular
228 enzyme activities, as described below. We ground soils to a fine powder using liquid N
229 and a mortar and pestle, and measured %C, %N, and $^{13}C$ using a Carlo Erba NA 1500
230 elemental analyzer (CE Instruments, Lancanshire, UK) coupled to a VG Isochrom
231 continuous flow isotope ratio mass spectrometer (Isoprime, Inc., Manchester, UK).
232
233 *2.5 Extractable nutrients and microbial biomass*
234
235 Microbial biomass and soil nutrient analyses were conducted following a modified
236 method described in Weintraub et al. (2007). We extracted samples and soil-free blanks
237 with 25 ml of 0.05 M potassium sulfate and agitated them on an orbital shaker for one
238 hour. To extract microbial biomass, we evenly distributed 2 ml of ethanol-free
239 chloroform over 5 g wet weight soil subsamples and incubated them at room temperature
240 for 24 hours in a stoppered 250 ml Erlenmeyer flask. Following incubation, we vented
241 flasks in a fume hood for at least 30 minutes until the chloroform had fully evaporated
242 (Witt et al., 2000). We filtered both control and fumigated samples through No. 1
243 Whatman paper and analyzed total extractable organic carbon (TOC) and total dissolved
244 nitrogen (TDN) with a Shimadzu TOC-L (Shimadzu Scientific Instruments, Inc.). We

245 measured extractable ammonium and nitrate with an Alpkem flow solution IV automated
246 wet chemistry system (O.I. Analytical College Station, TX). Total organic nitrogen
247 (TON) was calculated as the difference between TDN and total inorganic nitrogen (TIN =
248 ammonium + nitrate). We calculated extractable microbial biomass (MB) C and N as the
249 difference between paired chloroform-fumigated and non-fumigated subsamples and no
250 correction factors ($k_{ec}$) were applied (Weintraub et al., 2007).
251
252 To quantify the pool of soluble LMW-C and LMW-C incorporation in MB, we
253 lyophilized extracts of chloroform fumigated and non-fumigated subsamples using a
254 FreeZone 6 Liter console freeze dry system (Labcono, Kansas City, MO). We analyzed
255 lyophilized subsamples for %C and $\delta^{13}C$ with a Carlo Erba NA 1500 elemental analyzer
256 (CE Instruments, Lancanshire, UK) coupled to a VG Isochrom continuous flow isotope
257 ratio mass spectrometer (Isoprime, Inc., Manchester, UK), and applied the isotopic
258 mixing method as described below (see *Data Analysis*).
259
260 *2.6 Extracellular enzyme activities*
261
262 We assayed potential activities of seven hydrolytic extracellular enzymes (pEEA) [α-
263 Glucosidase (AG), β-Glucosidase (BG), Cellobiohydrolase (CB), and β-Xylosidase
264 (XYL), which are involved in C-acquisition, N-acetyl glucosaminidase (NAG) and
265 Leucine aminopeptidase (LAP), which are involved in N-acquisition, and Acid
266 phosphatase (AP), which is involved in P-acquisition] using the 96-well microplate
267 fluorometric method described in detail elsewhere (Bell et al., 2013; Koyama et al., 2013;

268 Wallenstein et al., 2009). Briefly, we homogenized 0.5 g of organic soil or 1.0 g of
269 mineral soil for 45 seconds with 91 ml of 50 mM sodium acetate buffer (pH 4.9) in a
270 Waring blender. Soil slurries were mixed on a stir plate and 800 µl subsamples were
271 added to a deep 96-well microplate using a wide orifice pipette tip for organic samples
272 and a narrow orifice pipette tip for mineral samples. Substrate concentrations, soil
273 masses, and incubation lengths were determined based on tests prior to the experiment in
274 order to capture the maximum potential enzyme activity ($V_{max}$). We pipetted 200 µl of
275 200 µM fluorescing substrate for all substrates—except AP, where we used 200 µl of 600
276 µM AP—into the sample assay wells and incubated them for three hours at 25°C. We
277 also prepared standards for each soil slurry using a range of concentrations of 4-
278 methylumbellifferone or 7-amino-4-methylcoumarin (LAP only). When the incubation
279 was complete, we centrifuged plates for three minutes at 1500 rpm (~350 xg) and
280 transferred 250 µl from each well into black 96-well plates. Substrate fluorescence was
281 measured on a Tecan Infinite M200 microplate reader at an excitation wavelength of 365
282 nm and an emission wavelength of 450 nm (Tecan Trading AG, Switzerland). Data are
283 presented as nmol g dry $soil^{-1}$ $hour^{-1}$.
284
285 *2.7 Data analysis*
286
287 We applied a two-source mixing model (Post, 2002) to assess the relative contribution of
288 native SOM C *versus* LMW-C to the C pool of interest (i.e., respired $CO_2$, microbial
289 biomass C, or bulk soil C), as follows:
290

$$f_{LMW\text{-}C} = (\delta_A - \delta_C) / (\delta_{LMW\text{-}C} - \delta_C),$$

where $f_{LMW\text{-}C}$ is the fraction of the C pool derived from $^{13}$C-glucose; $\delta_A$ and $\delta_C$ are the $\delta^{13}$C values of the C pool sampled from LMW-C amended and control collars, respectively; and $\delta_{LMW\text{-}C}$ is the $\delta^{13}$C of the 10 atom% glucose substrate. We calculated the fraction of the C pool derived from SOM as the difference between total and LMW-C-derived C pool. We defined the priming effect as a significant increase in SOM-derived respiration resulting from the input of LMW-C, and calculated it as the difference between treatment and control collar SOM-derived respiration (Kuzyakov, 2010). We defined microbial substrate use efficiency (SUE) as the partitioning of LMW-C between growth and respiration (Manzoni et al., 2012):

$$SUE = {}^{13}MB / ({}^{13}MB + {}^{13}CO_2),$$

where $^{13}$MB represents LMW-C assimilated in microbial biomass (g C m$^{-2}$), and $^{13}CO_2$ represents the fraction of LMW-C converted to $CO_2$ (g C m$^{-2}$). Similarly, we define substrate retention efficiency as the partitioning of LMW-C between bulk soils and respiration:

$$\text{Retention Efficiency} = {}^{13}C_{\text{Bulk Soil}} / ({}^{13}C_{\text{Bulk Soil}} + {}^{13}CO_2),$$

We performed all statistical analyses using R version 3.3.1. When necessary, we applied transformations to meet the assumptions of normality, evaluated with Shapiro-Wilk tests

314 and Q-Q plots. We used linear mixed-effect models to identify the main effects of
315 vegetation type, LMW-C amendment, and season, and all 2-way and 3-way interactions
316 on our dependent variable of interest using the lme4 package (Bates et al., 2016).
317 Similarly, we tested for main effects of depth, vegetation type, and treatment, conditional
318 on season (SI Table 2). Vegetation type, LMW-C amendment, season, depth, and all
319 interactions were included as categorical fixed effects, while our blocking design and
320 block interactions were included as categorical random effects. We also examined
321 whether amendment influenced LMW-C recovery in soil pools after 49 and 306 days of
322 incubation as above. Due to underlying heterogeneity in soil C stocks we conducted
323 additional analyses to confirm that our findings were robust. We include results from
324 models where soil C is included in the linear mixed-effect model as an additive covariate
325 (with no interactions) (SI Table 3) and results following normalization of all data to soil
326 C stocks ($g^{-1}$ soil C) (SI Table 4). Results from both models are consistent with values
327 scaled to collar area ($m^{-2}$). Therefore, we report all factor units in g $m^{-2}$ for the remainder
328 of this manuscript to correct for bulk density to 20 cm depth and allow direct comparison
329 of coefficients between treatments.
330
331 We used AICc model selection criteria for small sample sizes (Barton, 2016) to identify
332 factors driving the fraction of LMW-C converted to $CO_2$ and the proportion of LMW-C
333 retained belowground. If two variables were highly correlated (>0.5), one variable was
334 excluded from AICc model selection. As potential extracellular enzyme activities (pEEA)
335 were highly collinear, we used an initial AICc model selection including all seven pEEAs
336 against each dependent variable of interest. Finally, we built the full regression model

using extractable and non-extractable pools of C and N, organic and inorganic N, microbial biomass C and N, soil temperature, and AICc-selected pEEAs. Models with the lowest AICc score were considered to have the best fit.

## 3. Results

### *3.1 LMW-C amendment, month, and vegetation type effects on biogeochemical parameters*

In contrast to our hypothesis, we found no evidence of priming after LMW-C addition from soils underlying either vegetation type or in any month (Figure 2). Specifically, there was no significant main effect of treatment (LMW-C addition) or interaction (with month or vegetation) on SOM-derived $CO_2$ efflux (SI Table 5). However, SOM-derived $CO_2$ efflux was significantly influenced by month and was lower in September than July ($F_{2,15}$=7.94, p<0.01). Following LMW-C amendment, total $CO_2$ efflux (sum of LMW- and SOM- $CO_2$) exhibited significant interactions between vegetation type and treatment, as well as between treatment and month (SI Table 4). Overall, LMW-C amendment increased total $CO_2$ efflux by approximately 400% in *B. nana* soils and 650% in *E. vaginatum* soils relative to paired controls ($F_{2,36}$=8.36, p<0.001, Table 1). These results were consistent when accounting for soil C heterogeneity among plots, including soil C concentrations in the model (SI Table 3a), and normalizing values with soil C (SI Table 4). Additionally, LMW-C additions had the largest effect on total $CO_2$ efflux in May, and

were nine times higher from soils underlying *B. nana* and 14 times higher from soils underlying *E. vaginatum* relative to paired controls ($p<0.01$, Table 1).

*Figure 2*

MBC and pEEAs were influenced more by month than by treatment or vegetation type, and displayed no significant 2-way or 3-way interactions (Table 1, SI Table 6). MBC was significantly lower in May than July or September ($F_{2,36}=11.84$, $p<0.001$. There was a significant interaction between treatment and vegetation type for MBN ($F_{1,36}=5.90$, $p<0.05$), which was driven by higher biomass N in amended soils underlying *B. nana* in May than September. While MBC did not vary by soil depth or vegetation type in any season, MBN pools were 1.5 times higher in organic than mineral soils under both vegetation types in September ($F_{1,20}=5.46$, $p<0.05$, SI Table 2). BG was the only pEEA stimulated by LMW-C amendment ($F_{2,36}=8.54$, $p<0.01$), while XYL, NAG, and LAP varied significantly with season, exhibiting lower activities in May than other months (SI Table 6; $p<0.05$). There was a significant depth effect in July for all enzymes except NAG, and in May for all enzymes except XYL, where pEEAs were significantly higher in the organic than the mineral soil horizon. In September, we observed a significant interaction between depth and treatment, with activities of three C-cycling enzymes (BG, CB and XYL) stimulated by LMW-C amendment in the organic horizon. Activities for all other enzymes in September were significantly higher in the organic than mineral horizon.

382 We found a significant effect of month and LMW-C amendment on soil C pools, with no
383 significant interactions (Table 1). TOC exhibited a significant three-way interaction
384 between treatment, vegetation, and month ($F_{2,33}$=4.82, p<0.05), which was driven by
385 larger extractable C from soils underlying *B. nana* in July than May. Total soil C stocks
386 and TOC concentrations did not vary by depth (SI Table 2). All three soil N pools,
387 including soil N, TDN, and TIN exhibited significant interactions between vegetation
388 type and month (Table 1). Soil N stocks were 1.2 times greater in *B. nana* soils than *E.*
389 *vaginatum* soils in July, ($F_{2,33}$=4.56, p<0.05), but were not significantly different in other
390 months. N stocks in *B. nana* soils were significantly lower in September than July
391 (p<0.01). We observed a significant main effect of depth on soil N stocks, which were
392 nearly twice as large in the mineral horizon relative to the organic horizon in September
393 ($F_{1,20}$=6.44, p<0.05), and May ($F_{1,20}$=6.24, p<0.05, SI Table 2). Total dissolved N pools
394 were nearly twice as large in soils underlying *B. nana* in July and May than September,
395 and were also larger in *B. nana* than *E. vaginatum* soils during those months ($F_{2,33}$=3.79,
396 p<0.05). TDN concentrations were 3.5 times higher in the organic than mineral soil
397 horizons in July ($F_{1,22}$=6.86, p<0.05), but were three times higher in the mineral horizon
398 in September ($F_{1,22}$=5.66, p<0.05) and two times higher in May ($F_{1,22}$=3.99, p<0.05)
399 relative to the organic horizon (SI Table 2). TIN concentrations were twice as high in *B.*
400 *nana* soils in July compared to other months, and twice as high in *E. vaginatum* soils in
401 September compared to other months (p<0.05). We observed a significant main effect of
402 depth on TIN concentrations only in May, when availability was twice as high in the
403 mineral than organic soil horizons ($F_{1,20}$=4.95, p<0.05, SI Table 2).
404

405 *Table 1*

406

407 *3.2 Vegetation and season effects on the fate of LMW – C*

408

409 There were significant main effects of vegetation and month (no interaction) on LMW-
410 $CO_2$ efflux, which was 2.4 times higher from soils underlying *E. vaginatum* than *B. nana*
411 (Figure 2b,c; $F_{1,18}$=17.74, p<0.001), and higher in May than July (Figure 2a,c $F_{2,18}$=3.84,
412 p<0.05). There was a significant effect of vegetation on LMW-C retention efficiencies,
413 which were 1.5 times higher in soils underlying *B. nana* than *E. vaginatum* (Figure 3a;
414 $F_{1,18}$=4.63, p<0.01). Month significantly influenced microbial SUE, which was lowest in
415 September ($F_{2,18}$=7.83, p<0.01), with no effect of vegetation type or interactions between
416 month and vegetation type (Figure 3b, SI Table 5).

417

418 *Figure 3*

419

420 *3.3 Legacy effects of LMW-C addition*

421

422 Soils amended with LMW-C in July and measured after 49 and 306 days of *in situ*
423 incubation exhibited significant legacy effects (Figure 4). LMW-$CO_2$ losses were greater
424 from soils underlying *E. vaginatum* than *B. nana* after 10 and 49 days of incubation
425 (Figure 4a; $F_{1,34}$=11.88, p<0.01). Microbial SUE was highest after 10 days and negligible
426 49 and 306 days following amendment ($F_{2,34}$=19.80, p<0.001), while assimilation of
427 LMW-C in MB did not exhibit legacy effects (Figure 4b). In contrast, LMW-C retention

efficiencies were significantly greater 49 and 306 days following amendment than after 10 days (Figure 4c; $F_{2,34}$=32.78, p<0.001) under both vegetation types. SOM-derived respiration was not different than control systems and the priming effect was not observed during any measurement period.

*Figure 4*

3.4 *The influence of biogeochemical variables on LMW-C fate*

Explanatory variables controlling LMW-C conversion to $CO_2$, microbial SUE, and LMW-C retention in bulk soils were explored using AICc model selection (Figure 5). The best-fit model explaining LMW-$CO_2$ efflux included soil C:N, TOC:TDN, AP, soil C, and TOC (Figure 5a; full AICc model score: 182.90, best-fit AICc model score: 150.54). In contrast to our expectations, TOC exerted a larger influence (greater effect on AICc score) than N status (Figure 5a) and exhibited an inverse relationship with LMW-$CO_2$ efflux (p<0.001). Potential AP enzyme activities (nmol g dry soil$^{-1}$ MBC$^{-1}$) (p<0.05), soil C:N (p<0.05), and soil C (p<0.01) were also negatively related with LMW-$CO_2$ efflux, while TOC:TDN was positively related (p<0.05). The best-fit model explaining microbial SUE included soil temperature and TOC:TDN (Figure 5b, full AICc model score: 24.51, best-fit AICc model score: -3.7), suggesting a strong seasonal influence on metabolic efficiency. As predicted, the best-fit model explaining LMW-C retention efficiencies included MBC and extractable C:N (Figure 5c, full AICc model score: 21.93, best-fit model score: 2.51).

*Figure 5*

## 4. Discussion

Complex interactions among plants, soils, and microbes regulate soil C storage and the magnitude of the Arctic C-climate feedback. Currently, the dominant paradigm is that warming will alleviate temperature constraints on microbial activity and increase rates of decomposition and soil C loss to the atmosphere (Commane et al., 2017; Crowther et al., 2016; Mack et al., 2004; Mackelprang et al., 2011). However, our results highlight the exceptional C storage capacity of Arctic soils, and suggest shrub expansion could mitigate soil C losses to the atmosphere as the Arctic warms (Figure 1).

Plant traits, particularly rooting architecture and exudate production, strongly influence soil chemistry and the long-term stability of native SOM stocks (Jones et al., 2009; Zhu et al., 2016). Unlike *B. nana* shrubs, *E. vaginatum* tussocks do not form ectomycorrhizal (ECM) associations, and their soil microbial communities have been shown to become progressively N-limited throughout the growing season (McMahon and Schimel, 2017). *E. vaginatum* also produce lower quality fine root litter with a 30% higher C:N ratio than those produced by *B. nana* (Hobbie, 1996; Sullivan et al., 2007), likely contributing to the lower N concentrations we observed in tussock relative to shrub soils. Tussock roots can extend from the soil surface to the permafrost interface (Iversen et al., 2015) and directly supply mineral soils with labile C, which is expected to stimulate microbial

474 mining of nutrients from SOM (Chen et al., 2013) and induce a positive priming effect, as
475 previously observed in several laboratory incubation studies (Fontaine et al., 2004; Wild
476 et al., 2014). On the other hand, shrub expansion is predicted to shift rooting distributions
477 upward into the organic horizon (Iversen et al., 2015), where minimal or negligible
478 priming has been observed in laboratory studies (Fontaine et al., 2007; Wild et al., 2014).
479 Taken together, this suggests that a shallower root distribution with shrub expansion
480 should reduce TOC and N availability at depth. Our data, however, do not support this.
481 Rather, we found significantly higher N concentrations, particularly in mineral soils
482 colonized by *B. nana* shrubs, and no differences between in TOC concentration between
483 soil horizons. Additionally, pEEAs were significantly lower in mineral relative to organic
484 soil horizons, which could explain a lack of priming in mineral soils. Overall, greater
485 LMW-C retention in shrub soils suggests shrub expansion may increase microbial
486 activity and C-cycling in the priming-resistant organic horizon, and increase N
487 availability at depth, where priming might otherwise occur.
488
489 Plant litter quality and soil chemistry control microbial SUE, which in turn regulate
490 mechanisms of SOM formation and retention (Cotrufo et al., 2013; Dijkstra et al., 2015).
491 We found that apparent SUE tended to be higher in soils underlying *B. nana*, resulting in
492 significantly greater LMW-C retention, particularly after nine months of incubation. As
493 high-quality shrub litter more closely matches microbial stoichiometry (Chen et al., 2013)
494 shrub expansion may facilitate stabilization of microbial products within the soil matrix
495 (Dohnalkova et al., 2017; Schmidt et al., 2011). Although we did not observe SOM
496 priming, the conversion of LMW-C to $CO_2$ was twice as high from soils underlying *E.*

497 *vaginatum,* indicating activation of catabolic pathways and preferential transfer of new C
498 sources to the atmosphere. Potential activities of BG, an extracellular enzyme involved in
499 C-acquisition, also increased following LMW-C addition in tussock soils. While
500 increased activities of C-targeting enzymes do not support positive priming effects
501 associated with the nutrient mining hypothesis (Chen et al., 2013; Rousk et al., 2016),
502 they do indicate mineralization of C-rich substrates, potentially from turnover of tussock
503 litter. Laboratory incubation experiments have shown that the *potential* for priming exists
504 in a wide range of soils. But these experiments often add a high substrate concentration at
505 a single time point that do not closely mimic constant inputs of lower concentration
506 through root exudation (Cheng *et al.*, 2003; Fontaine *et al.*, 2003; Brant *et al.*, 2006;
507 Blagodatskaya & Kuzyakov, 2008; Pisani *et al.*, 2016). Thus, it is unclear from these
508 experiments whether priming will be stimulated by increased C inputs in critical systems
509 like Arctic tundra. In this first *in situ* experiment conducted in the Arctic, we did not find
510 strong evidence of priming. However, our addition of a single, energy-rich substrate, may
511 have been utilized by a subset of the microbial community that is not representative of
512 the slower-growing communities typically associated with SOM priming (Fontaine and
513 Barot, 2005) that utilize the full chemical diversity of root exudate compounds. The lack
514 of mycorrhizal associations with *E. vaginatum* tussocks could explain the negligible
515 priming effects we observed, as the production of oxidative enzymes by fungal
516 communities are considered to be a rate-limiting step for SOM mineralization (Rousk et
517 al., 2014). While shrub-colonized soils have greater fungal abundance and enzymatic
518 potential for SOM priming, higher soil N concentrations can reduce microbial production
519 of extracellular enzymes targeting complex organic matter (Carreiro et al.,

2000). Additionally, the co-addition of C and N has been shown to stimulate N-mineralization from SOM by up to 300% in Arctic soils (Rousk et al., 2016); if we had amended soils with a more complex substrate we may have induced a positive priming effect (Fontaine and Barot, 2005). Thus, we cannot rule out the possibility of priming as this system changes.

Our results confirm the importance of seasonal sampling in the Arctic, as interactions between season and vegetation type controlled the fate of LMW-C. When LMW-C was added to shrub soils in May, a large proportion was retained belowground. This retention may be caused by greater microbial assimilation of labile C during spring thaw, and production of microbial necromass, which contributes to relatively stable mineral associated organic matter (MAOM) and SOM formation (Averill and Waring, 2017; Cotrufo et al., 2013; Schmidt et al., 2011). In contrast, LMW-C additions in tussock soils were largely emitted back to the atmosphere as $CO_2$. In July, the influence of LMW-C amendments was reduced, with significantly lower LMW-$CO_2$ production from soils underlying both vegetation types. Greater belowground rhizosphere inputs during peak plant productivity may reduce microbial reliance upon exogenous LMW-C. In shrub soils, higher activities of N and P acquiring extracellular enzymes, indicate greater nutrient accessibility (Wallenstein et al., 2009), which can lead to more efficient microbial communities (McLaren et al., 2017) and the stabilization of microbial-derived products belowground (Dohnalkova et al., 2017; Tfaily et al., 2014). During fall senescence, C-rich plant litter is deposited at the soil surface, while roots are actively acquiring and translocating nutrients belowground (Chapin and Bloom, 1976; Iversen et

543 al., 2015). During this period, extracellular enzyme activities were highest in soils
544 underlying both vegetation types, perhaps indicating sufficient nutrient availability for
545 enzyme production, litter depolymerization, and SOM decomposition (McMahon and
546 Schimel, 2017; Wallenstein et al., 2009). While seasonal dynamics provide important
547 insights on short-term mechanisms controlling the fate of new C, it remains critical to
548 determine whether these responses are transient or of sufficient duration and magnitude
549 to influence the C-climate feedback.
550
551 Few studies have examined the longer-term fate of new C inputs in the Arctic,
552 significantly limiting certainty surrounding the interaction of climate warming and shrub
553 expansion on C cycling. During the initial stages of *in situ* incubation, microbial
554 communities underlying both vegetation types respired LMW-C derived $CO_2$ to the
555 atmosphere. However, less than half of the LMW-C added was respired from beneath
556 either vegetation type, potentially as a result of efficient metabolism and SOM formation
557 (Blagodatskaya and Kuzyakov, 2008; Cotrufo et al., 2015; Hill et al., 2008). After two
558 months of *in situ* incubation, LMW-C incorporation in microbial biomass pools and
559 conversion to $CO_2$ did not differ relative to control systems, however after ten months
560 LMW-$CO_2$ efflux was significantly greater from soils underlying *E. vaginatum* relative to
561 *B. nana*. While it is unlikely that LMW-C substrate remained untransformed within the
562 dissolved SOM pool (Dijkstra et al., 2015; Hill et al., 2008), predation within the
563 rhizosphere and turnover of microbial products may contribute to longer-term LMW-C
564 derived efflux (Moore et al., 2003). More significantly, the proportion of LMW-C
565 retained in the soil *versus* lost as $CO_2$ was higher in soils underlying *B. nana,* which

566 could indicate efficient SOM stabilization via microbial assimilation of dissolved organic
567 matter and retention of microbial byproducts (Cotrufo et al., 2015). While further work is
568 needed to determine the long-term stability and efficiency of C transformation through
569 metabolic pathways, our longer-term perspective provides evidence that new C inputs
570 contribute to SOM formation, particularly in shrub-dominated soils. This effect could be
571 strengthened as climate warming thaws permafrost soils and exposes mineral surfaces
572 able to stabilize microbial products (Schmidt et al., 2011; Wieder et al., 2013).
573
574 Our observations of lower $CO_2$ efflux and higher substrate retention in shrub-dominated
575 soils may not be ubiquitous—as their expansion will not entirely eliminate other plant
576 species (Elmendorf et al., 2012; Livensperger et al., 2016)—and may not persist
577 throughout time. As the climate changes, microbial access to soil substrates and SOM
578 stability will be regulated by the interactions between soil moisture and temperature. The
579 years in which we conducted the *in situ* priming experiment were representative of
580 longer-term seasonal treads, however hydrologic connectivity has been projected to
581 increase with high-latitude warming (Rowland et al., 2010). Currently, shrubs are
582 expanding into areas with high potential for moisture accumulation and drainage,
583 specifically valley slopes and floodplains (Naito and Cairns, 2011). Local landscape
584 characteristics, including the balance between thermokarst formation (Abbott and Jones,
585 2015) *versus* hillslope drainage (Kittler et al., 2018), will influence microbial
586 accessibility to substrates, and the balance between SOM priming and formation.
587 Substrate availability is positively correlated with moisture, as enhanced pore
588 connectivity facilitates SOC transport from protected to active C pools, where it can be

metabolized by microorganisms (Bailey et al., 2017). Similarly, warmer soil temperatures are associated with increased rates of SOM mineralization (Crowther et al., 2016; Hartley et al., 2008), although additional stressors may induce transient (Allison et al., 2010; Sistla et al., 2013), or even negative (Allison and Treseder, 2008) responses. Therefore, the complex interplay between soil temperature and moisture conditions, which were not exhaustively captured in this study, may alter the balance between SOM retention and priming.

In conclusion, we found that LMW-C conversion to $CO_2$ and retention in the soil matrix is influenced by a number of biogeochemical parameters relating primarily to nutrient availability. Specifically, soils underlying shrubs have higher soil N concentrations and greater retention of added glucose, likely a function of the stoichiometric controls on microbial SUE. In contrast, the activity of C-degrading enzymes and conversion of new LMW-C inputs to $CO_2$ suggests the cycling of labile C is rapid in the C-rich soils underlying *E. vaginatum.* These results support our hypothesis that soil N status and access to labile energy sources, such as root exudates, will determine the fate of new C sources in the Arctic. While large-scale CLM models predict C storage in the Arctic will decrease under warming scenarios (Crowther et al., 2016; Thornton et al., 2009; Wieder et al., 2013), our results suggest shrub expansion may mitigate turnover of new C sources. Thus, the interactions between shrubs and microbial metabolic efficiency act as critical controls on the direction and magnitude of the Arctic C-climate feedback.

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612

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623 **Cited Literature**

624


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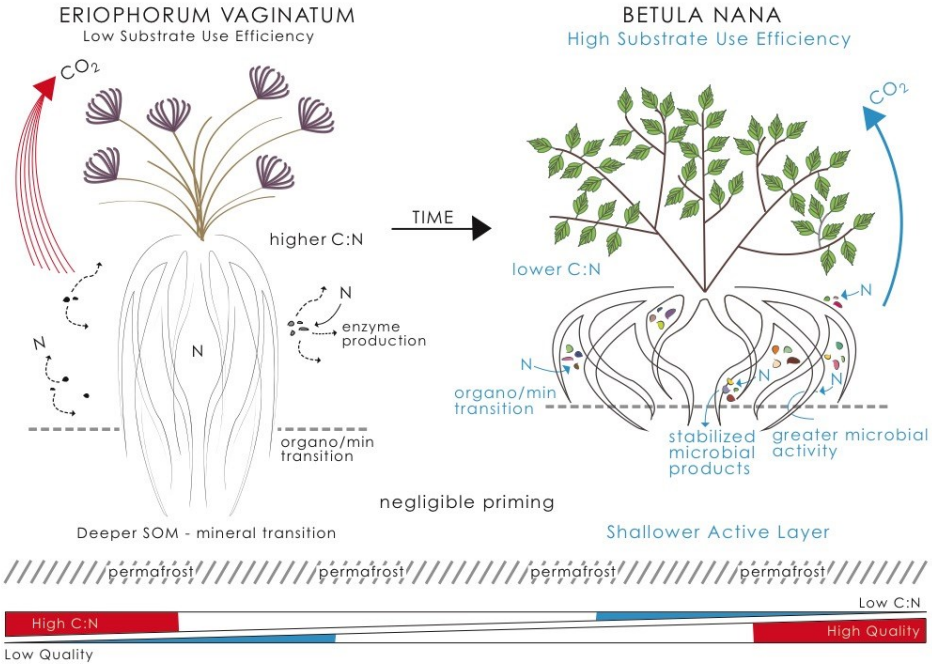



950
951 **Fig. 1** Conceptual model depicting the fate of LMW-C as influenced by vegetation type and soil chemistry.
952 Plant traits (e.g. litter chemistry, root architecture, depth to mineral horizon) influence soil chemistry and
953 lead to divergent microbial functions. Higher microbial substrate use efficiencies in soils underlying *B.*
954 *nana* contribute to soil organic matter formation. Arrow sizes indicate the magnitude of $CO_2$ efflux.

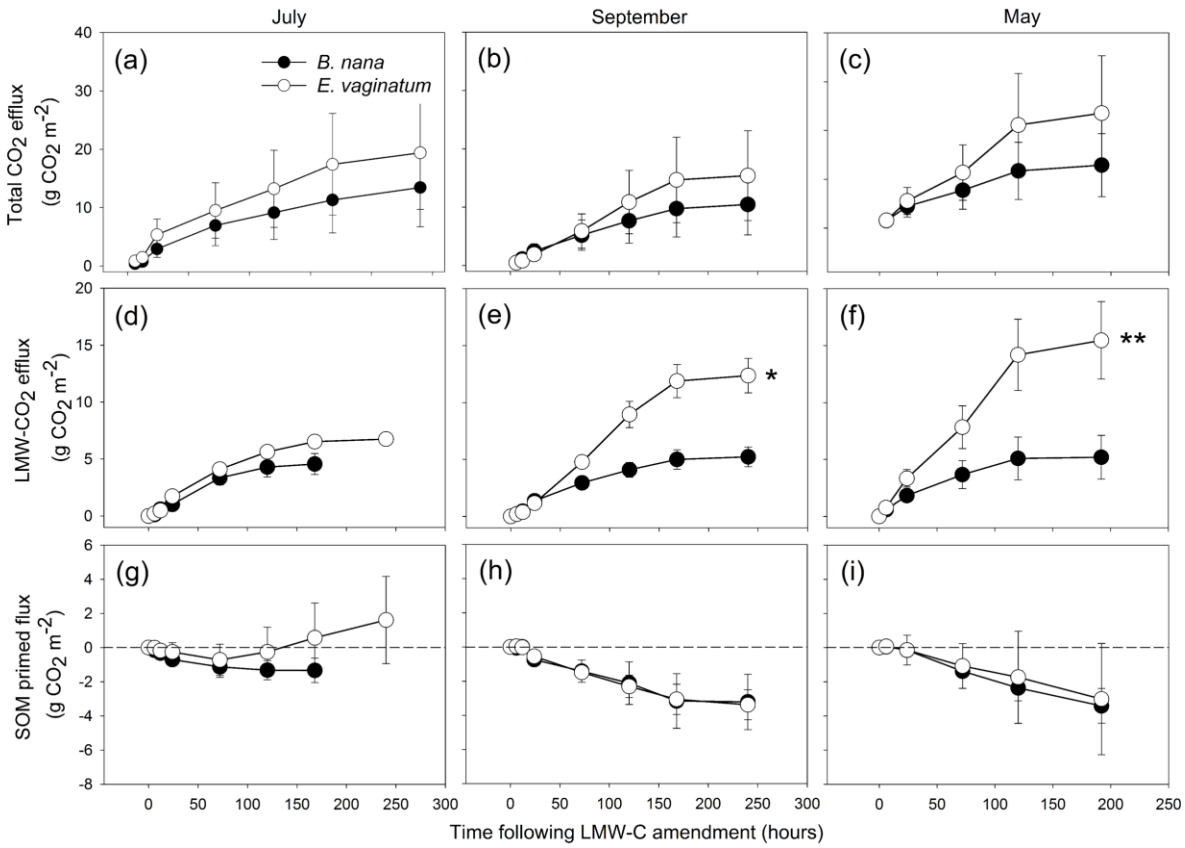
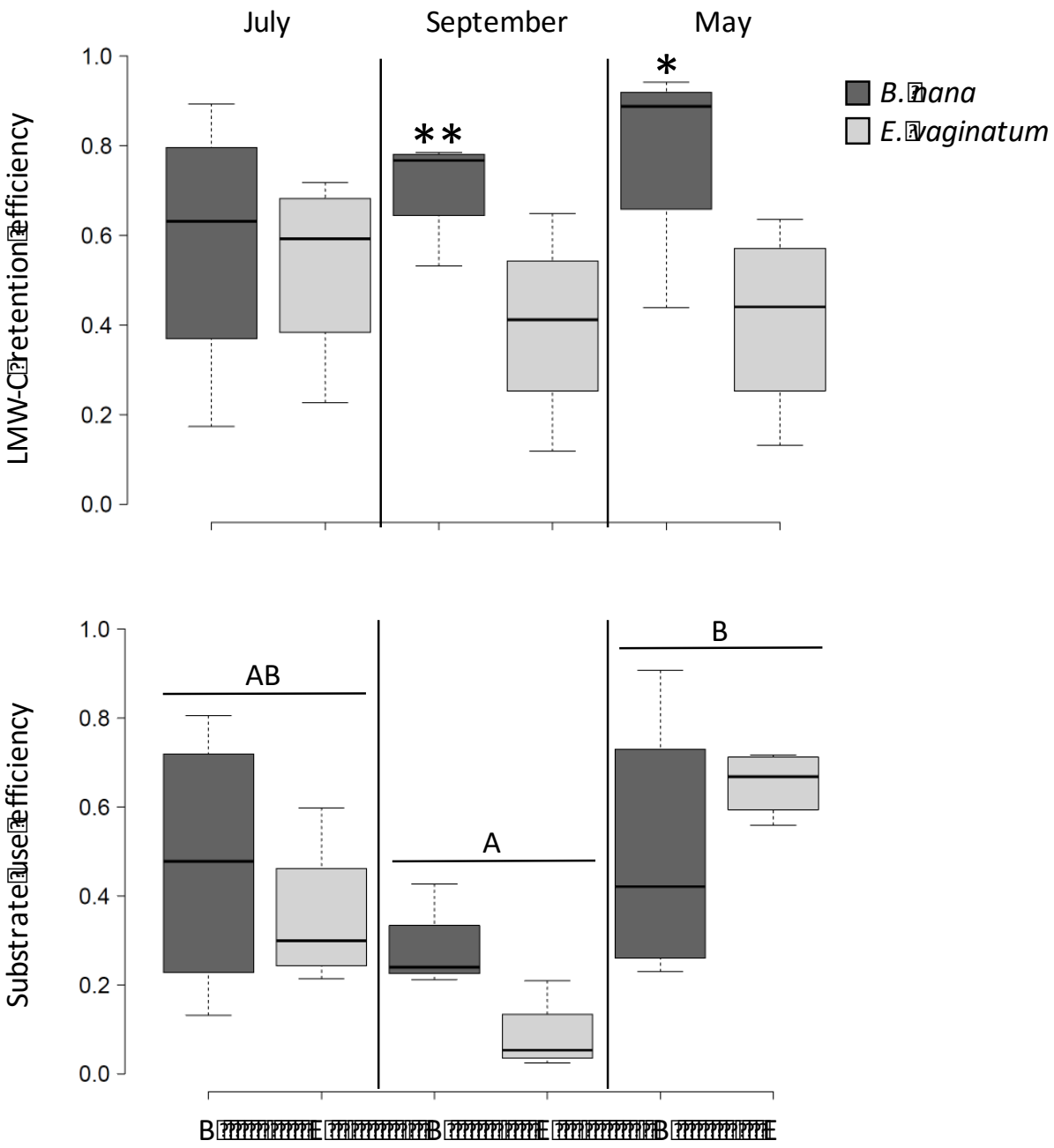



**Fig. 2.** Cumulative respiration from soils underlying *B. nana* (closed symbols) and *E. vaginatum* (open symbols). Total $CO_2$ efflux (g $m^{-2}$) (upper panel) in July (a), September (b), and May (c), $CO_2$ efflux (g $m^{-2}$) derived from LMW-C (middle panel) in July (d), September (e), and May (f), and the difference between amendment and control $CO_2$ efflux (lower panel) in July (g), September (h), and May (i). Values below y=0 on SOM primed flux y-axis indicate negative priming (or SOM formation), while values above indicate positive priming (excess C lost as $CO_2$ in amended compared to control soils resulting from metabolism of native SOM stocks). Points represent means ± standard error (n=4). Significant differences between vegetation type and LMW-C treatment are reported as * $p < 0.05$, or ** $p < 0.01$.




964
965 **Fig. 3.** Boxplots representing LMW-C retention efficiencies (a) and substrate use efficiencies (b) by
966 vegetation type and month for short-term (10 day) incubation periods. *B. nana* (B) are displayed in charcoal
967 boxes, and *E. vaginatum* (E) in light gray boxes. Significant differences between vegetation type are
968 reported as * $p < 0.05$, or ** $p < 0.01$. Significant differences between months are indicated by letters
969 ($p<0.05$). There were no significant interactions between month and LMW-C amendment. Each box spans
970 the interquartile range and whiskers extend to the minimum and maximum of the distribution (n=4).

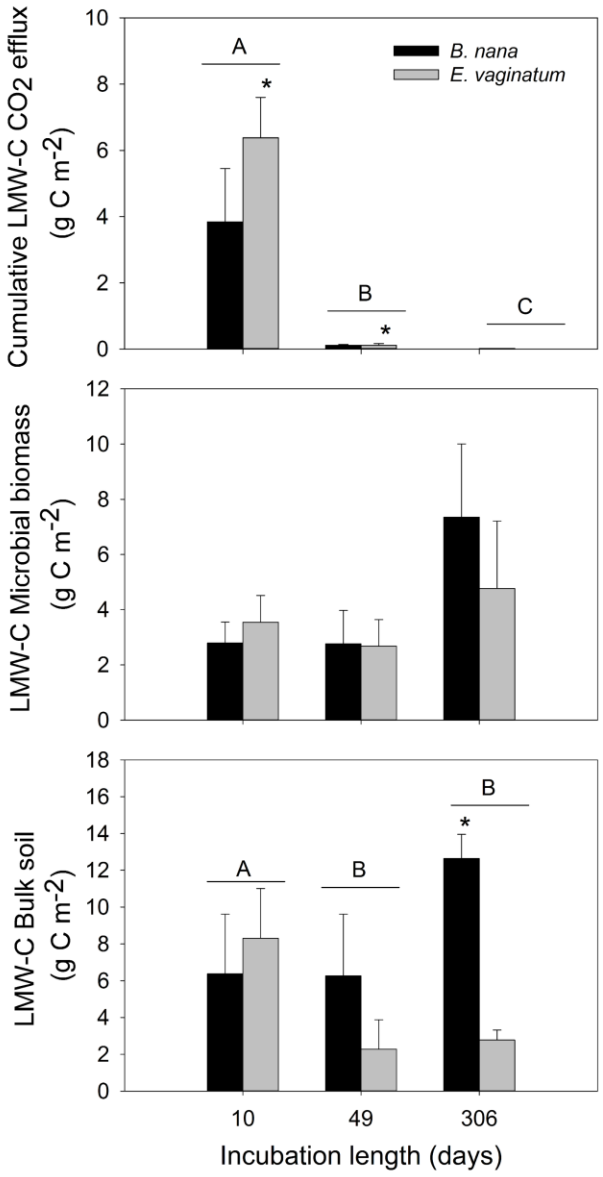
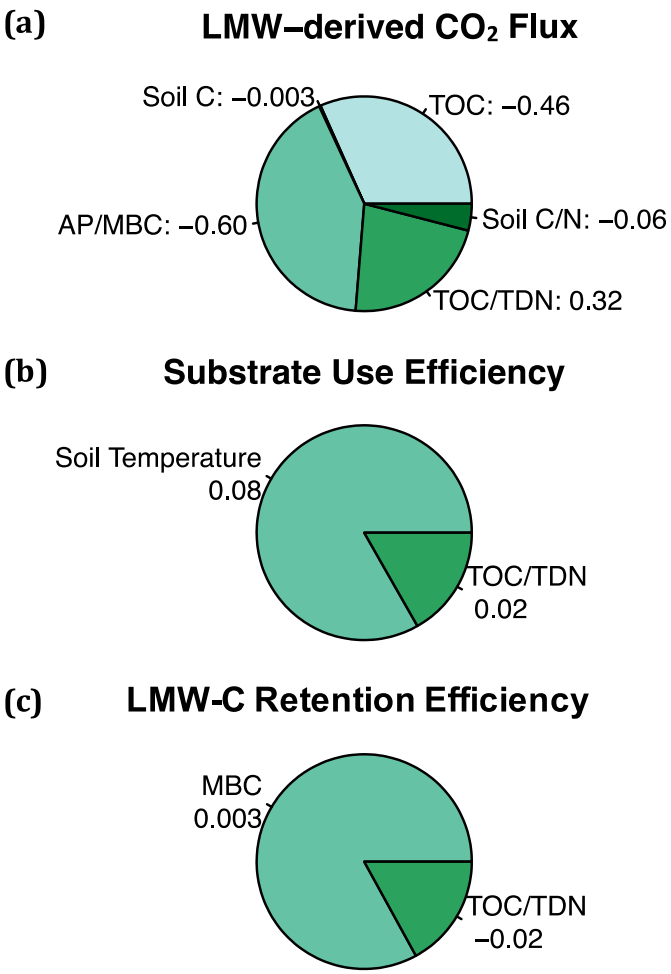



**Fig. 4.** Legacy effect of LMW-C measured after 10 (short), 49 (intermediate), and 306 (long) days of *in situ* incubation. *B. nana* are shown in black and *E. vaginatum* are shown in light gray. Panels represent cumulative LMW-C derived $CO_2$ efflux (a), LMW-C assimilation in microbial biomass (b), and LMW-C recovery in bulk soil (c) relative to a non-amended control. Bars represent means (g $^{13}C$-$CO_2$ $m^{-2}$) ± standard error (n=4). Significant differences between vegetation type are reported as * $p < 0.05$, or ** $p < 0.01$. Significant differences between months are indicated by letters ($p<0.05$). There were no interactions between month and LMW-C amendment.




979

980 **Fig. 5.** Pie charts display the coefficient strength of biogeochemical parameters included in best-fit AICc-

981 selected models for LMW-derived $CO_2$ flux (a), microbial substrate use efficiency (b), and LMW-C

982 retention efficiency (c). Selected parameters include soil and dissolved pools of C and N (Soil C, Soil N,

983 TOC, TDN), microbial biomass C (MBC), activity of acid phosphatase relative to MBC (AP/MBC), and

984 soil temperature at 5 cm depth (°C).

985 **Table 1** Biogeochemical characteristics of soils underlying *B. nana* and *E. vaginatum*. The average
986 followed by the standard error (± 1 S.E.) in parentheses for total $CO_2$ efflux, soil C and N, dissolved C and
987 N (TOC, TDN), and microbial biomass C and N (MBC, MBN) (n=4). The level of significance from the 3-
988 way ANOVA model including vegetation (V), treatment (T), month (M), all 2-way and 3-way interactions
989 are reported as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, or non-significant (ns).
990

| Month | Vegetation/ Treatment | $CO_2$ Flux ($g\ m^{-2}$) | Soil C ($g\ m^{-2}$) | Soil N ($g\ m^{-2}$) | TOC ($g\ m^{-2}$) | TDN ($g\ m^{-2}$) | TIN ($ug\ m^{-2}$) | MBC ($g\ C\ m^{-2}$) | MBN ($g\ N\ m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|
| July | *B. nana* | | | | | | | | |
| | Control | 5.70 (0.44) | 2788.98 (310.12) | 85.95 (7.64) | 27.48 (2.40) | 1.88 (0.56) | 10.98 (5.91) | 59.18 (13.74) | 7.13 (2.04) |
| | Amended | 12.12 (2.88) | 3407.54 (223.61) | 94.04 (14.46 | 10.87 (3.55) | 1.62 (0.45) | 44.62 (16.42) | 51.41 (6.99) | 6.02 (0.76) |
| | *E. vaginatum* | | | | | | | | |
| | Control | 6.93 (0.55) | 2859.55 (382.04) | 44.61 (9.45) | 13.41 (1.35) | 0.60 (0.05) | 4.80 (1.90) | 55.25 (11.53) | 4.97 (1.17) |
| | Amended | 19.41 (1.73) | 2919.19 (287.17) | 63.62 (17.54) | 11.88 (1.34) | 0.72 (0.14) | 7.08 (1.99) | 67.84 (12.35) | 11.20 (3.49) |
| September | *B. nana* | | | | | | | | |
| | Control | 7.79 (1.03) | 1658.17 (330.93) | 21.02 (11.13) | 10.09 (3.74) | 0.74 (0.21) | 4.34 (1.89) | 44.94 (25.34) | 3.07 (1.49) |
| | Amended | 10.46 (0.49) | 2551.58 (429.46) | 70.46 (13.79) | 8.50 (1.27) | 0.75 (0.18) | 4.65 (2.51) | 36.81 (8.11) | 4.03 (1.38) |
| | *E. vaginatum* | | | | | | | | |
| | Control | 5.77 (0.64) | 2104.85 (385.80) | 43.92 (12.37) | 10.01 (1.32) | 0.70 (0.11) | 11.53 (5.75) | 55.84 (18.25) | 4.50 (1.48) |
| | Amended | 15.41 (2.02) | 3335.89 (137.46) | 76.43 (5.43) | 9.36 (1.78) | 0.86 (0.29) | 18.34 (7.68) | 41.74 (6.50) | 4.21 (0.68) |
| May | *B. nana* | | | | | | | | |
| | Control | 1.45 (0.23) | 2002.79 (333.86) | 68.05 (15.60) | 28.05 (4.68) | 1.45 (0.36) | 10.64 (3.32) | 118.18 (13.74) | 9.35 (0.69) |
| | Amended | 12.90 (2.17) | 2086.96 (456.49) | 71.15 (19.01) | 14.48 (2.73) | 1.57 (0.59) | 14.75 (6.76) | 111.28 (38.76) | 7.96 (2.40) |
| | *E. vaginatum* | | | | | | | | |
| | Control | 1.66 (0.22) | 1882.44 (679.71) | 39.20 (12.06) | 14.17 (3.71) | 0.66 (0.13) | 3.28 (0.87) | 53.66 (17.24) | 4.64 (1.66) |
| | Amended | 23.55 (5.90) | 3233.73 (306.74) | 76.73 (11.75) | 26.86 (4.72) | 1.13 (0.11) | 8.04 (2.98) | 155.54 (30.50) | 9.32 (1.39) |
| Source of variance | | | | | | | | | |
| T | | *** | ** | *** | * | ns | ns | ns | ns |
| V | | ** | ns | ns | ns | ** | ns | ns | ns |
| M | | *** | * | ns | *** | * | ns | *** | ** |
| T*V | | ** | ns | ns | *** | ns | ns | ns | * |
| T*M | | *** | ns | ns | ns | ns | ns | ns | ns |
| V*M | | ns | ns | * | ns | * | * | ns | ns |
| T*V*M | | ns | ns | ns | * | ns | ns | ns | ns |

991
992

**Supplemental Information**

**Supplemental Table 1.** Average annual soil temperatures at the surface, or 5 cm, 10 cm, or 20 cm belowground, and cumulative precipitation for 2014, 2015, and the ten-year average (2005-2015).

| Year | Surface soil temperature (°C) | Soil temperature at 5 cm (°C) | Soil temperature at 10 cm (°C) | Soil temperature at 20 cm (°C) | Cumulative precipitation (mm) |
|---|---|---|---|---|---|
| 2014 | 5.2 (0.1) | 5.7 (0.2) | 3.4 (0.1) | 3.4 (0.1) | 238.8 |
| 2015 | 5.4 (0.1) | 6.8 (0.2) | 4.2 (0.1) | 4.1 (0.1) | 209.3 |
| 10-year average | 5.6 (0.2) | 5.8 (0.2) | 3.5 (0.1) | 3.1 (0.1) | 206.3 |

**Supplemental Table 2.** Biogeochemical characteristics of organic and mineral soil horizons underlying *B. nana* and *E. vaginatum* (conditional on month). The average followed by the standard error (± 1 S.E.) in parentheses for soil C and N, dissolved C and N (DOC, TDN), and microbial biomass C and N (MBC, MBN) (n=4). The level of significance from the 3-way ANOVA model including soil depth (D), vegetation (V), treatment (T), all 2-way and 3-way interactions are reported as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, or non-significant (ns).

**July**

| Depth | Vegetation/ Treatment | Soil C ($g\ m^{-2}$) | Soil N ($g\ m^{-2}$) | TOC ($g\ m^{-2}$) | TDN ($g\ m^{-2}$) | TIN ($g\ m^{-2}$) | MBC ($g\ m^{-2}$) | MBN ($g\ m^{-2}$) |
|---|---|---|---|---|---|---|---|---|
| Lower | *B. nana* | | | | | | | |
| | Control | 2634.49 (875.21) | 114.63 (33.40) | 7.38 (3.48) | 0.91 (0.47) | 11.46 (7.67) | 12.49 (8.40) | 3.33 (1.38) |
| | Amended | 4255.49 (530.57) | 148.20 (8.89) | 5.72 (3.93) | 1.09 (0.48) | 17.90 (11.29) | 27.96 (19.90) | 3.78 (2.65) |
| | *E. vaginatum* | | | | | | | |
| | Control | 3385.44 (1467.15) | 42.40 (16.96) | 3.84 (1.42) | 0.21 (0.08) | 5.63 (2.43) | 21.16 (10.24) | 2.07 (1.09) |
| | Amended | 2911.85 (762.47) | 117.36 (41.66) | 2.06 (0.59) | 0.13 (0.01) | 2.47 (0.86) | 14.79 (5.10) | 1.59 (0.44) |
| Upper | *B. nana* | | | | | | | |
| | Control | 2401.40 (34.00) | 57.28 (7.96) | 6.39 (2.03) | 0.23 (0.07) | 1.99 (1.11) | 26.81 (11.58) | 3.04 (1.38) |
| | Amended | 2415.64 (44.44) | 51.29 (16.92) | 2.38 (1.17) | 0.16 (0.05) | 26.59 (14.71) | 9.15 (3.46) | 1.01 (0.51) |
| | *E. vaginatum* | | | | | | | |
| | Control | 2120.01 (72.31) | 38.28 (12.00) | 2.12 (1.32) | 0.07 (0.04) | 1.14 (0.83) | 6.71 (3.44) | 0.63 (0.38) |
| | Amended | 2436.32 (32.61) | 26.14 (5.28) | 3.02 (0.60) | 0.19 (0.08) | 4.19 (2.06) | 14.65 (3.82) | 2.96 (1.24) |
| D | | ns | *** | ns | ns | * | ns | ns |
| V | | ns | * | ns | ns | ** | ns | ns |
| T | | ns | ns | ns | ns | ns | ns | ns |
| D*V | | ns | ns | ns | ns | ns | ns | ns |
| D*T | | ns | ns | ns | ns | ns | ns | ns |
| V*T | | ns | ns | ns | ns | ns | ns | ns |
| D*V*T | | ns | ns | ns | ns | ns | ns | ns |

**SEPTEMBER**

| Depth | Vegetation/ Treatment | Soil C (g $m^{-2}$) | Soil N (g $m^{-2}$) | TOC (g $m^{-2}$) | TDN (g $m^{-2}$) | TIN (g $m^{-2}$) | MBC (g $m^{-2}$) | MBN (g $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|
| Lower | *B. nana* | | | | | | | |
| | Control | 837.86 (342.95) | 12.93 (2.00) | 0.87 (0.29) | 0.12 (0.04) | 1.74 (0.64) | 2.69 (0.89) | 0.10 (0.07) |
| | Amended | 2319.04 (1076.70) | 80.14 (34.12) | 1.92 (1.44) | 0.24 (0.13) | 4.16 (2.06) | 2.48 (1.21) | 0.42 (0.15) |
| | *E. vaginatum* | | | | | | | |
| | Control | 1857.14 (707.02) | 58.05 (23.25) | 2.67 (1.15) | 0.21 (0.56) | 11.09 (7.16) | 13.01 (7.17) | 1.17 (0.61) |
| | Amended | 4249.82 (266.17) | 115.91 (11.22) | 2.80 (1.09) | 0.56 (0.31) | 19.22 (9.90) | 9.69 (3.61) | 0.93 (0.40) |
| Upper | *B. nana* | | | | | | | |
| | Control | 1452.39 (629.49) | 27.50 (19.15) | 1.98 (0.96) | 0.09 (0.03) | 3.14 (1.79) | 12.62 (10.15) | 0.83 (0.56) |
| | Amended | 2242.58 (41.30) | 53.87 (3.53) | 1.76 (0.46) | 0.09 (0.03) | 1.46 (0.86) | 8.97 (3.47) | 0.96 (0.48) |
| | *E. vaginatum* | | | | | | | |
| | Control | 1877.90 (303.74) | 29.53 (7.30) | 1.79 (0.74) | 0.09 (0.03) | 3.49 (1.19) | 11.11 (3.80) | 0.95 (0.43) |
| | Amended | 2322.94 (52.22) | 30.96 (12.44) | 2.45 (0.35) | 0.11 (0.01) | 1.60 (0.12) | 12.14 (1.11) | 1.27 (0.16) |
| D | | ns | * | ns | * | ns | ns | * |
| V | | * | ns | ns | ns | * | ns | ns |
| T | | ** | ** | ns | ns | ns | ns | * |
| D*V | | ns | ns | ns | ns | ns | ns | ns |
| D*T | | ns | ns | ns | ns | ns | ns | ns |
| V*T | | ns | ns | ns | ns | ns | ns | ns |
| D*V*T | | ns | ns | ns | ns | ns | ns | ns |

**MAY**

| Depth | Vegetation/ Treatment | Soil C (g $m^{-2}$) | Soil N (g $m^{-2}$) | TOC (g $m^{-2}$) | TDN (g $m^{-2}$) | TIN (g $m^{-2}$) | MBC (g $m^{-2}$) | MBN (g $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|
| Lower | *B. nana* | | | | | | | |
| | Control | 1438. 41 (713.34) | 73.56 (37.31) | 4.86 (1.72) | 0.42 (0.26) | 6.71 (4.16) | 15.34 (5.99) | 1.09 (0.66) |
| | Amended | 1973.06 (739.63) | 102.91 (35.05) | 5.14 (2.23) | 0.94 (0.44) | 14.85 (6.59) | 24.52 (13.22) | 2.62 (1.51) |
| | *E. vaginatum* | | | | | | | |
| | Control | 2068.51 (1391.96) | 50.27 (31.61) | 2.85 (1.60) | 0.18 (0.10) | 1.38 (0.54) | 21.87 (17.49) | 1.96 (1.75) |
| | Amended | 3689.49 (773.18) | 102.80 (24.69) | 7.13 (2.00) | 0.55 (0.21) | 9.43 (4.53) | 48.31 (14.87) | 3.74 (1.20) |
| Upper | *B. nana* | | | | | | | |
| | Control | 1951.19 (165.00) | 53.95 (3.47) | 6.95 (0.82) | 0.42 (0.19) | 7.35 (5.37) | 41.21 (8.22) | 3.29 (0.60) |
| | Amended | 1899.22 (442.18) | 52.35 (11.82) | 4.30 (1.31) | 0.29 (0.08) | 4.37 (2.29) | 46.92 (28.02) | 2.72 (0.96) |
| | *E. vaginatum* | | | | | | | |
| | Control | 1641.00 (502.48) | 30.79 (6.95) | 3.34 (1.10) | 0.12 (0.03) | 1.29 (0.13) | 9.88 (3.30) | 0.92 (0.30) |
| | Amended | 2466.89 (46.92) | 50.91 (3.40) | 7.13 (1.58) | 0.20 (0.03) | 0.98 (0.13) | 39.41 (9.67) | 1.99 (0.26) |
| D | | ns | * | ns | ns | * | ns | ns |
| V | | ns | ns | ns | ns | * | ns | ns |
| T | | ns | ns | ns | ns | ns | * | * |
| D*V | | ns | ns | ns | ns | ns | ns | ns |
| D*T | | ns | ns | ns | ns | * | ns | ns |
| V*T | | ns | ns | * | ns | ns | * | ns |
| D*V*T | | ns | ns | ns | ns | ns | ns | ns |

**Supplemental Table 3a.** Biogeochemical characteristics of soils underlying *B. nana* and *E. vaginatum* for total $CO_2$ efflux, LMW-C conversion to $CO_2$, soil organic matter-derived $CO_2$ (SOM-$CO_2$), priming-derived $CO_2$ (primed pool and %), microbial substrate use efficiency (SUE), LMW-C stabilization (Stab. Eff.), dissolved C, total N, inorganic N (TOC, TDN, TIN), and microbial biomass C and N (MBC, MBN) (n=4). All values are reported on a g $m^{-2}$ basis, unless otherwise noted. The level of significance from the 3-way ANOVA model including vegetation (V), treatment (T), month (M), all 2-way and 3-way interactions are reported as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, or non-significant (ns). The level of significance from the 3-way ANOVA model for soil C is reported numerically with bolded text for significant results.

| Source of variance | $CO_2$ Flux | LWM C-$CO_2$ | SOM-$CO_2$ | Priming (%) | SUE | Stab. Eff. | TOC | TDN | TIN (ug $m^{-2}$) | MBC | MBN |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Soil C | 0.94 | 0.31 | 0.99 | 0.78 | 0.51 | 0.38 | 0.23 | 0.18 | **0.02** | **0.001** | 0.06 |
| T | *** | | | | | | * | ns | ns | ns | ns |
| V | ** | *** | ns | ns | ns | * | ns | *** | ns | ns | ns |
| M | *** | ns | ** | ns | ** | ns | *** | ns | ns | *** | ** |
| T*V | ** | | | | | | *** | ns | ns | ns | ns |
| T*M | *** | | | | | | ns | ns | ns | ns | ns |
| V*M | ns | ns | ns | ns | ns | ns | ns | ns | * | ns | ns |
| T*V*M | ns | | | | | | * | ns | ns | ns | ns |

**Supplemental Table 3b.** Biogeochemical characteristics of soils underlying *B. nana* and *E. vaginatum* where microbial biomass C (MBC) and total inorganic N (TIN) are normalized to soil C content ($g^{-1}$ soil C). The level of significance from the 3-way ANOVA model including vegetation (V), treatment (T), month (M), all 2-way and 3-way interactions are reported as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, or non-significant (ns).

| Source of variance | MBC (g C $g^{-1}$ soil C) | TIN (µg N $g^{-1}$ soil C) |
|---|---|---|
| T | ns | ns |
| V | ns | ns |
| M | *** | ns |
| T*V | ns | ns |
| T*M | ns | ns |
| V*M | ns | * |
| T*V*M | ns | ns |

**Supplemental Table 4.** Biogeochemical characteristics of soils underlying *B. nana* and *E. vaginatum* normalized to soil C. The average followed by the standard error (± 1 S.E.) in parentheses for soil C and N, dissolved C and N (TOC, TDN), and microbial biomass C and N (MBC, MBN) (n=4). All values are reported on a g per gram soil C basis. The level of significance from the 3-way ANOVA model including treatment (T), vegetation (V), and month (M), all 2-way and 3-way interactions are reported as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, or non-significant (ns).

| Month | Vegetation/ Treatment | $CO_2$ | DOC | Soil N | TDN | TIN | MBC | MBN |
|---|---|---|---|---|---|---|---|---|
| July | *B. nana* | | | | | | | |
| | Control | 2.11 (0.25) | 10.53 (2.03) | 31.08 (0.99) | 0.73 (0.25) | 0.004 (0.002) | 22.64 (7.41) | 2.71 (0.99) |
| | Amended | 3.54 (0.76) | 3.19 (0.96) | 28.1 (4.83) | 0.46 (0.11) | 0.012 (0.005) | 15.48 (2.79) | 1.77 (0.19) |
| | *E. vaginatum* | | | | | | | |
| | Control | 2.64 (0.56) | 5.08 (1.06) | 15.56 (2.09) | 0.23 (0.05) | 0.002 (0.001) | 18.54 (1.97) | 1.65 (0.24) |
| | Amended | 6.67 (0.18) | 4.32 (0.88) | 23.09 (8.21) | 0.26 (0.07) | 0.002 (0.001) | 23.96 (5.53) | 4.04 (1.51) |
| September | *B. nana* | | | | | | | |
| | Control | 5.93 (2.28) | 5.29 (1.67) | 13.89 (7.91) | 0.42 (0.06) | 0.002 (0.001) | 23.69 (12.10) | 1.61 (0.69) |
| | Amended | 4.47 (0.82) | 3.64 (0.93) | 27.92 (3.14) | 0.32 (0.10) | 0.002 (0.001) | 15.33 (3.25) | 1.63 (0.45) |
| | *E. vaginatum* | | | | | | | |
| | Control | 3.11 (0.73) | 5.15 (0.86) | 19.45 (3.83) | 0.40 (0.12) | 0.005 (0.002) | 23.58 (5.47) | 1.95 (0.57) |
| | Amended | 7.57 (2.16) | 8.69 (1.87) | 23.63 (2.48) | 0.35 (0.02) | 0.002 (0.001) | 48.73 (10.42) | 2.88 (0.41) |
| May | *B. nana* | | | | | | | |
| | Control | 0.78 (0.16) | 15.32 (3.72) | 33.17 (1.90) | 0.95 (0.29) | 0.005 (0.002) | 65.71 (16.93) | 5.08 (0.89) |
| | Amended | 8.57 (3.72) | 7.19 (0.41) | 34.22 (3.15) | 0.67 (0.16) | 0.006 (0.002) | 55.44 (17.97) | 3.60 (0.54) |
| | *E. vaginatum* | | | | | | | |
| | Control | 0.57 (0.06) | 4.93 (1.31) | 13.20 (3.26) | 0.23 (0.04) | 0.001 (0.00) | 18.61 (5.81) | 1.57 (0.49) |
| | Amended | 4.60 (0.49) | 2.77 (0.45) | 23.16 (2.36) | 0.25 (0.08) | 0.005 (0.002) | 12.45 (1.81) | 1.25 (0.18) |
| T | | *** | * | ** | ns | ns | ns | ns |
| V | | ns | ns | ** | *** | ns | ns | ns |
| M | | *** | ** | ns | ns | ns | *** | ** |
| T*V | | * | * | ns | ns | ns | ns | ns |
| T*M | | *** | ns | ns | ns | ns | ns | ns |
| V*M | | ns | ns | ** | ns | ** | ns | ns |
| T*V*M | | ns | * | * | ns | ns | ns | ns |

**Supplemental Table 5.** LMW-C fate in soils underlying *B. nana* and *E. vaginatum*. The average followed by the standard error (± 1 S.E.) in parentheses for LMW-C conversion to $CO_2$, soil organic matter-derived $CO_2$ (SOM-$CO_2$), priming-derived $CO_2$ (primed pool and %), microbial substrate use efficiency (SUE), and LMW-C stabilization (n=4). The level of significance from the 2-way ANOVA model including vegetation (V) and month (M), and all 2-way interactions are reported as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, or non-significant (ns).

| Month | Vegetation/ Treatment | LWM C-$CO_2$ (g $m^{-2}$) | SOM-$CO_2$ (g $m^{-2}$) | Primed (g $m^{-2}$) | Primed (% ) | SUE | Stab. Eff. |
|---|---|---|---|---|---|---|---|
| July | *B. nana* | | | | | | |
| | Amended | 3.85 (3.22) | 8.27 (1.28) | 8.27 (1.28) | -17.12 (16.64) | 0.47 (0.15) | 3.06 (1.83) |
| | *E. vaginatum* | | | | | | |
| | Amended | 6.38 (1.22) | 13.03 (2.65) | 13.02 (2.65) | 5.36 (15.35) | 0.35 (0.09) | 1.46 (0.48) |
| September | *B. nana* | | | | | | |
| | Amended | 5.23 (1.75) | 5.23 (0.71) | 5.23 (0.71) | -30.44 (14.50) | 0.28 (0.05) | 2.85 (0.58) |
| | *E. vaginatum* | | | | | | |
| | Amended | 12.37 (3.03) | 3.04 (0.94) | 3.04 (0.94) | -24.54 (7.03) | 0.09 (0.04) | 0.84 (0.36) |
| May | *B. nana* | | | | | | |
| | Amended | 5.19 (3.84) | 7.71 (1.17) | 7.71 (1.17) | -29.95 (10.40) | 0.50 (0.15) | 8.20 (3.14) |
| | *E. vaginatum* | | | | | | |
| | Amended | 15.46 (6.81) | 8.09 (2.80) | 8.09 (2.80) | -23.11 (16.07) | 0.66 (0.04) | 0.88 (0.34) |
| Source of variance | | | | | | | |
| V | | *** | ns | ns | ns | ns | ** |
| M | | * | ** | ns | ns | ** | ns |
| V*M | | ns | ns | ns | ns | ns | ns |

**Supplemental Table 6.** Potential extracellular enzyme activities of soils underlying *B. nana* and *E. vaginatum*. The average followed by the standard error (± 1 S.E.) in parentheses for seven hydrolytic enzymes (n=4). Potential activities are reported in nmol activity g dry soil$^{-1}$ hr$^{-1}$. The level of significance from the 3-way ANOVA model including vegetation (V), treatment (T), month (M), all 2-way and 3-way interactions are reported as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, or non-significant (ns).

| Month | Vegetation / Treatment | CB | AG | BG | XYL | LAP | NAG | AP |
|---|---|---|---|---|---|---|---|---|
| July | *B. nana* | | | | | | | |
| | Control | 4553.48 (742.21) | 429.23 (142.10) | 1040.04 (257.82) | 570.59 (125.84) | 2537.18 (920.81) | 141.85 (23.36) | 8217.36 (1223.42) |
| | Amended | 3615.39 (729.55) | 231.98 (73.78) | 545.76 (117.62) | 477.95 (76.49) | 2375.87 (395.55) | 207.36 (46.47) | 10453.93 (2975.87) |
| | *E. vaginatum* | | | | | | | |
| | Control | 1572.87 (240.63) | 159.90 (57.36) | 330.38 (101.56) | 358.78 (93.74) | 798.31 (399.16) | 75.86 (13.93) | 5153.81 (1737.06) |
| | Amended | 2898.37 (402.32) | 213.91 (37.59) | 900.59 (253.43) | 389.36 (43.37) | 1059.70 (200.97) | 87.33 (21.19) | 4209.36 (318.81) |
| September | *B. nana* | | | | | | | |
| | Control | 965.42 (438.27) | 191.50 (174.21) | 86.62 (67.14) | 237.67 (120.37) | 1007.64 (651.01) | 109.51 (56.13) | 5679.99 (3230.04) |
| | Amended | 3107.00 (596.83) | 311.35 (75.88) | 689.92 (253.43) | 462.17 (102.17) | 1477.13 (375.88) | 147.00 (3.35) | 6369.95 (1179.31) |
| | *E. vaginatum* | | | | | | | |
| | Control | 2392.63 (721.80) | 232.58 (81.94) | 305.14 (148.47) | 419.46 (128.81) | 947.87 (305.70) | 130.27 (39.71) | 4568.26 (1326.97) |
| | Amended | 3989.83 (316.60) | 265.08 (99.44) | 1087.86 (263.10) | 673.41 (164.01) | 1710.74 (351.47) | 158.745 (24.62) | 7288.91 (1628.80) |
| May | *B. nana* | | | | | | | |
| | Control | 689.70 (182.05) | 70.31 (23.03) | 186.15 (81.17) | 103.54 (19.62) | 456.15 (94.69) | 38.60 (1.37) | 1301.82 (83.57) |
| | Amended | 913.95 (203.89) | 205.48 (121.58) | 350.60 (75.90) | 247.45 (112.64) | 565.99 (113.28) | 58.10 (3.51) | 1469.47 (426.73) |
| | *E. vaginatum* | | | | | | | |
| | Control | 869.40 (197.59) | 191.83 (121.52) | 351.53 (101.87) | 270.70 (109.53) | 500.93 (155.44) | 35.20 (3.95) | 872.61 (211.27) |
| | Amended | 651.19 (61.00) | 185.27 (141.23) | 246.78 (11.98) | 219.89 (126.47) | 456.37 (48.07) | 41.02 (4.66) | 977.80 (147.40) |
| Source of variance | | | | | | | | |
| T | | ns | ns | ** | ns | ns | ns | ns |
| V | | * | ns | ns | ns | ns | ns | ns |
| M | | ns | ns | ns | ** | *** | *** | ns |
| T*V | | ns | ns | ns | ns | ns | ns | ns |
| T*M | | ns | ns | ns | ns | ns | ns | ns |
| V*M | | ns | ns | ns | ns | * | ns | ns |
| T*V*M | | ns | ** | ns | ns | ns | ns | ns |