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1 **Hiding in the background: community-level patterns in invertebrate** 2 **herbivory across the tundra biome**

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44

45 **Abstract**

46 Invertebrate herbivores depend on external temperature for growth and metabolism. Continued warming
47 in tundra ecosystems is proposed to result in increased invertebrate herbivory. However, empirical data
48 about how current levels of invertebrate herbivory vary across the Arctic is limited and generally
49 restricted to a single host plant or a small group of species, so predicting future change remains
50 challenging. We investigated large-scale patterns of invertebrate herbivory across the tundra biome at the
51 community level and explored how these patterns are related to long-term climatic conditions and year-
52 of-sampling weather, habitat characteristics and aboveground biomass production. Utilizing a
53 standardized protocol, we collected samples from 92 plots nested within 20 tundra sites during summer
54 2015. We estimated the community-weighted biomass lost based on the total leaf area consumed by
55 invertebrates for the most common plant species within each plot. Overall, invertebrate herbivory was
56 prevalent at low intensities across the tundra, with estimates averaging 0.94% and ranging between 0.02%
57 and 5.69% of plant biomass. Our results suggest that mid-summer temperature influences the intensity of
58 invertebrate herbivory at the community level, consistent with the hypothesis that climate warming should
59 increase plant losses to invertebrates in the tundra. However, most of the observed variation in herbivory
60 was associated with other site level characteristics, indicating that other local ecological factors also play

61 an important role. More details about the local drivers of invertebrate herbivory are necessary to predict
62 the consequences for rapidly changing tundra ecosystems.

63 **Keywords:** background herbivory, biomass loss, climate change, community-weighted average,
64 invertebrate, insects, tundra

65

66 **Introduction**

67 Invertebrate herbivores can have strong effects on the structure and function of Arctic ecosystems. Most
68 studies of invertebrate herbivory in high-latitude systems have focused on outbreak events, when
69 herbivores consume massive amounts of plant biomass over a short time period. Outbreaks have most
70 frequently been reported for boreal forests and the forest-tundra ecotone (Jepsen et al. 2013; Karlsen et al.
71 2013; Kaukonen et al. 2013) whereas few have been described in true tundra systems (Post and Pedersen
72 2008; Lund et al. 2017). In contrast, under non-outbreak densities, invertebrates are responsible for low
73 but chronic biomass removal, referred to as background herbivory (Kozlov and Zvereva 2017). At these
74 low densities the immediate effects of invertebrates appear minimal (Kotanen and Rosenthal 2000), but
75 the longer-term nature of background herbivory may have prolonged effects on plant growth (Zvereva et
76 al. 2012), community interactions (Barrio et al. 2013), and nutrient fluxes (Metcalf et al. 2016). The
77 current understanding of the patterns of background invertebrate herbivory in tundra environments is
78 based on only a few studies that focused on either a single host plant species (*Betula glandulosa-nana*
79 complex, Barrio et al. 2017) or on specific growth forms (shrubs, Kozlov et al. 2015a). No studies have
80 assessed patterns of invertebrate background herbivory at the community level across the tundra biome.

81 The interaction between invertebrate herbivores and plants in tundra ecosystems occurs under
82 environmental conditions characterized by cold temperatures, a short growing season, and precipitation
83 that falls mostly as snow (Strathdee and Bale 1998). Current trends associated with rapid climate change
84 at high latitudes indicate that the tundra biome will continue to experience increased temperature and
85 altered precipitation regimes, as well as a longer growing season (Post et al. 2009; IPCC 2013; Overland
86 et al. 2017). Invertebrate ecophysiology strongly depends on temperature, so even moderate increases in
87 temperature have the potential to alter the duration of the life cycles (or parts of them) of invertebrate
88 herbivores, increase their densities and activity (Asmus et al. 2018), or alter their distribution ranges or
89 those of their competitors (Hodkinson and Bird 1998; Bale et al. 2002; Bolduc et al. 2013). For example,
90 higher summer temperatures can increase the intensity of herbivory (Birkemoe et al. 2016), create
91 phenological mismatches between specialist herbivores and plant species (Kharouba et al. 2015) or

92 alternatively, induce stronger phenological matches between plants and herbivores (Jepsen et al. 2011;
93 Pureswaran et al. 2019), and/or alter herbivore feeding choices (Barrio et al. 2016a), although these
94 patterns are far from being general in either space or time (Kozlov and Zvereva 2015; Zvereva et al. 2016;
95 Kozlov et al. 2017). Moreover, changes in precipitation could affect the amount of damage caused by
96 invertebrate herbivores indirectly, through their influence on leaf traits, such as leaf toughness (based on
97 the structural materials that make up the leaf) or leaf chemistry. Stress due to dry conditions can either
98 increase the toughness of leaves, thus decreasing their palatability for invertebrate herbivores (Onoda et
99 al. 2011) or induce plants to decrease the production of herbivore defense chemicals, resulting in an
100 increase in the palatability of leaf tissues (Berg et al. 2008). Kozlov et al. (2015b) found that precipitation
101 contributed to latitudinal patterns observed in invertebrate herbivory, such that increased precipitation
102 resulted in higher levels of invertebrate-caused defoliation. With the potential for so many different
103 responses to climate change, it is essential to document the existing patterns of invertebrate herbivory and
104 to explore the drivers behind these patterns in order to predict future changes.

105 The level of herbivory on plants can also be driven by local site characteristics, such as habitat type,
106 productivity or plant community composition. Herbivory is generally lower in more diverse plant
107 communities, but this varies with the host specificity of insects, and plant species composition may be
108 more important than species richness *per se* (Jactel and Brockerhoff 2007). For example, different growth
109 forms or functional groups of plants differ in their palatability and responses to herbivory (Turcotte et al.
110 2014). In general, deciduous shrubs are more palatable than evergreen shrubs (MacLean Jr. and Jensen
111 1985; Turcotte et al. 2014), and shrubs, due to plant apparency, tend to be consumed more than
112 herbaceous plants (Turcotte et al. 2014). Graminoid species are often less palatable due to lower
113 nutritional content and stronger physical defenses (Tschardt and Greiler 1995). Thus, local and site
114 level factors influencing variation in herbivory need to be considered in combination with climate drivers.

115 We assessed invertebrate herbivory within vascular plant communities across the tundra biome to
116 investigate the role of climatic drivers, specifically temperature and precipitation, habitat, and
117 aboveground plant biomass, in explaining the variation in plant losses to invertebrate herbivores. We
118 predicted that higher levels of invertebrate herbivory would be associated with sites experiencing higher
119 summer temperatures and higher precipitation, and would vary across habitats with different aboveground
120 biomass availability, such that sites with more plant biomass will experience higher levels of herbivory
121 (Bonser and Reader 1995). We also assessed the hypothesis that different plant functional groups
122 (deciduous shrub, evergreen shrub, graminoid, herbs) experience different levels of herbivory due to
123 differences in palatability, such that deciduous shrubs would have more damage than evergreen shrubs,
124 shrubs would have more damage than herbaceous plants, and that herbs would have more damage than

125 graminoids. To do this we examined invertebrate herbivory at the species level for 42 vascular plant
126 species grouped into broad functional groups. To our knowledge, this is the first survey of community
127 level invertebrate herbivory in the tundra. Our coordinated study may provide a framework for future
128 global monitoring efforts of invertebrate herbivory in other ecosystems too.

129

130 **Methods**

131 *Study design*

132 This study was conducted during the summer of 2015 and involved researchers working at 20
133 Arctic/alpine tundra sites in the Northern Hemisphere (**Figure 1**). In order to ensure consistent data
134 collection, we adopted a common protocol designed by the Herbivory Network (Barrio et al. 2016b;
135 **Online Resource 1**) that provided a simple, hierarchical design for sampling individual plants and plots
136 within each study site. The protocol was distributed to members of the Herbivory Network who generally
137 selected locations associated with their own long-term research efforts; these sites are described in more
138 detail in Rheubottom (2018). Sites spanned high-latitude tundra ecosystems ranging from 55.24 to 78.60
139 °N and one alpine site in the Swiss Alps (Val Bercla 46.47 °N).

140 A study site was broadly defined as an area of 0.25-25 km² where sampling was conducted. At each site,
141 the dominant habitat type was identified, avoiding areas influenced by extremes in moisture, soil
142 chemistry, or disturbances, so that study sites would represent a variety of habitats characteristic of the
143 tundra biome (**Table 1**). Habitat types were determined based on the broader habitat categories defined in
144 the Circumpolar Arctic Vegetation Map (CAVM; Walker et al. 2005), or were classified as alpine tundra.
145 Latnjajaure was included in the erect-shrub tundra category based on a similar definition from Virtanen et
146 al. (2016). Overall, a total of 6 habitat types were considered (**Table 1**).

147 At each site, five plots (20 × 20 m) were established at least 100 m apart. Three focal species of vascular
148 plants were identified in each plot based on their overall contribution to the community-wide foliar
149 biomass, with the exception of Toolik Lake where five focal species were sampled (**Table 1**).

150 Consequently, the focal species were plot-specific and could differ between plots within the same study
151 site. In total, 42 focal species were sampled across all sites, including 13 graminoids, 9 deciduous shrubs,
152 8 evergreen shrubs, and 12 herbs (**Table 2**).

153 *Sampling protocol*

154 Three individual plants for each of the focal species at each plot were identified. Plants were considered
155 different “individuals” when they were at least 10 m apart. Leaf samples (ca. 100 leaves per plant
156 individual) were collected from each individual. In the case of plants that did not have enough leaves,
157 samples were collected from “aggregates”, i.e. multiple stems growing close together (within 1–2 m). The
158 selection of individuals or aggregates was undertaken from a distance of 5–10 m to avoid recognition of
159 invertebrate herbivory during the selection process and avoid confirmation bias (i.e. picking individuals
160 specifically because they were damaged or undamaged; Kozlov et al. 2014). In many cases, branches or
161 stems were collected to avoid damaging leaves by detaching them in the field, or missing leaves with a
162 large amount of damage (i.e. only the petiole remaining). Samples were press-dried as herbarium
163 specimens and sent for analysis by the first author.

164 The contribution of each of the focal species to the biomass in each plot was estimated using the point-
165 intercept method. In each plot, 16 sampling points were placed in a regular grid 5 m apart. Point-intercept
166 data were collected at each sampling point using a 50 × 50 cm frame with ten fixed pin positions. The
167 number of times a focal species touched each pin was recorded (i.e. multiple hits per pin per focal species
168 were possible). Three of the sampling points were randomly selected to harvest total aboveground plant
169 biomass using the same frame, after the point-intercept data were collected. Biomass samples were stored
170 in paper bags and air-dried in the field; in the lab, biomass samples were sorted into the three focal
171 species recorded for each plot and ‘other’ biomass, and weighed to the nearest mg.

172 The sampling points that had both point-intercept and biomass data were used to calculate a conversion
173 factor to estimate plant biomass based on point intercept data as described by Bråthen and Hagberg (2004;
174 **Online Resource 2**). Biomass estimates for each focal species in each plot were then calculated based on
175 the 16 sampling points, multiplying the mean number of hits per pin of each of the focal species by the
176 corresponding conversion factor.

177 *Leaf damage assessment*

178 Leaf sample preparation involved detaching the leaves from the branches/stems or, for graminoids, at the
179 ligule. All leaves were sampled starting from the uppermost one on each branch/stem, until the desired
180 number of leaves was obtained. A dissecting microscope was used to observe leaves for damage. Each
181 leaf was examined on both sides with a light source shining down on to the leaf to assess external
182 damage, and then, both sides were examined with a light source shining up through the leaf to evaluate
183 internal damage (Barrio et al. 2017). Leaf mine damage was identified by the presence of invertebrates
184 inside the mines, while galls that were unclear were reviewed by entomologists at the University of
185 Alberta.

186 The percent area of each leaf that was damaged by invertebrates (either chewing or skeletonization caused
187 by external feeders, mining, or gall damage) was visually attributed to one of the following damage
188 categories: intact leaves, <1%, 1-5%, 5-25%, 25-50%, 50-75%, and >75% of leaf area damaged or
189 removed by herbivores (Kozlov 2008; Barrio et al. 2017). When two different types of invertebrate
190 herbivory were present on the same leaf (3.3% of leaves), the second damage type (smaller percentage)
191 was recorded as secondary damage and included in the analysis (see below), but the leaf was not counted
192 twice in the total number of leaves. Data for the damage assessment of *Betula nana* was previously used
193 in Barrio et al. (2017) which focused on examining variation in invertebrate herbivory for a single species
194 complex across the Arctic.

195 *Calculation of community weighted estimates of biomass lost (CWBL)*

196 As an approximation of foliar loss to invertebrate herbivores, the percent leaf area damaged (PLAD) was
197 calculated as the mean leaf area damaged for each of the focal species in a plot. The number of leaves in
198 each damage category was multiplied by the median value of damage in that category (for example, a leaf
199 in the 25-50% bin was assigned as having 37.5% damage), summed over all damage categories and
200 divided by the total number of leaves in the sample (Barrio et al. 2017).

201 The community weighted biomass lost (CWBL, %) due to total invertebrate leaf damage was calculated
202 for each plot (**Online Resource 3**), taking into account the proportion of biomass contributed by each of
203 the focal species, and how much of this was consumed by invertebrates, as estimated by PLAD. CWBL
204 takes into account the effect of different species composition at different study sites, and allows for
205 comparisons across sites with different habitat types. In order to control for the biomass of the focal
206 species being only a proportion of the total community biomass, the percent contribution of each focal
207 species to the total biomass was incorporated into the CWBL calculation. In the case of Toolik Lake, no
208 total biomass harvest data was available but five focal species were reported; it was assumed that these
209 five focal species represented most of the biomass at the community level and the contribution of each
210 focal species to the biomass of these five focal species was included in the CWBL calculations (**Online**
211 **Resource 3**). CWBL was expressed as a percentage of the total biomass in a plot to control for the
212 variation in biomass across tundra sites, from polar deserts to shrub tundra.

213 *Statistical analyses*

214 The combined leaf damage caused by different feeding guilds of invertebrate herbivores (defoliators,
215 miners and gallers) was used in our analysis because some types of leaf damage, such as mining or
216 galling, tend to be infrequent in tundra (Barrio et al. 2017). The variation in CWBL was analyzed using

217 Linear Mixed Effects Models (LMM) (Zuur et al. 2009), including study site as a random factor to
218 account for the study design of multiple plots sampled within each site. Predictor variables included
219 climatic variables (long-term mean July temperature and precipitation, and July 2015 temperature and
220 precipitation relative to the long-term average), total plant biomass per m², and the habitat type of the
221 study site (**Table 1; Online Resource 3**). Temperature and precipitation data were compiled from the
222 CRU TS3.10 Dataset (Harris et al. 2014), and divided into long-term July means (based on data from
223 1990-2015) and the deviations from the respective means in July 2015. Long-term means incorporated
224 interannual variation in temperature and precipitation, while the 2015 values indicated deviations in the
225 weather conditions during the sampling year relative to the long-term average (i.e. if the summer 2015
226 was colder and/or wetter than average at a particular site). July was used to indicate mid-summer
227 conditions that coincide with peak temperatures and peak plant biomass (Myers-Smith et al. 2015; Barrio
228 et al. 2017). The six different habitats included wetlands, erect-shrub tundra, prostrate-shrub tundra,
229 barren tundra, graminoid tundra, and alpine tundra (**Table 1**).

230 Five models were constructed (**Table 3**) based on our *a priori* hypotheses that herbivory would be driven
231 by: 1) the long-term mean July temperature; or by more additional variables: 2) the long-term mean
232 precipitation, 3) the 2015 deviations from average temperature and precipitation, 4) aboveground plant
233 biomass or 5) habitat type. The five models were compared using AICc values (**Table 3**). Collinearity
234 between the predictors was assessed across the 20 sites, and only combinations of variables with
235 correlations $r < |0.55|$ were included in the models (**Table 3**). Running the analyses with and without the
236 alpine site and with and without Murmansk, which showed the largest value of CWBL (**Figure 2**) did not
237 change the results, so these sites were retained in the analyses.

238 In a separate analysis, we examined whether different plant growth forms and/or functional groups
239 experienced different levels of invertebrate herbivory. Using a Welch's two-sample t-test, we compared
240 woody plants to herbaceous plants, deciduous shrubs to evergreen shrubs, and herbs to graminoids.

241 Model assumptions were checked by visually examining plots of the residuals versus fitted values to
242 determine homoscedasticity of variances; normality of residuals was examined via QQ-plots. In order to
243 meet the assumptions the CWBL values were log₁₀-transformed prior to analysis. All statistical analyses
244 were carried out in R 3.5.1 (R Development Core Team 2017), and LMMs were built using the *lme4*
245 package (Bates et al. 2015).

246

247 **Results**

248 *Distribution of damage among herbivore feeding guilds*

249 Invertebrate damage was found in 9,062 of 77,586 leaves examined (11.7%). The majority of damaged
250 leaves (7,265 or 80.2%) had feeding marks of externally defoliating invertebrates. We found only 772
251 mined leaves and 1,025 leaves with insect or mite galls (8.5% and 11.3% of all damaged leaves,
252 respectively). Damage by defoliators was recorded in leaves of 35 of the 42 focal plant species, by leaf
253 miners in 21 species, and by gall-forming herbivores in 21 species (**Table 2**).

254 *Variation in herbivory among focal species*

255 The 42 focal species included in our analyses experienced varying levels of invertebrate herbivory. The
256 highest average percent leaf area damaged (PLAD) from all samples combined was 26.05% (*Vaccinium*
257 *myrtillus*), while seven plant species had no invertebrate damage at all (**Table 2**). Only 13 species
258 experienced leaf area losses greater than 1%, with only three of those species experiencing more than 5%
259 (*V. myrtillus*, *Salix reticulata* (9.13%), and *Oxyria digyna* (6.13%); **Table 2**).

260 We found differences in invertebrate herbivory between plant growth forms and/or functional groups.
261 Foliar losses of woody plants were four times higher than that of herbaceous plants (2.93% vs. 0.70%;
262 $t_{561.42}=5.16$, $p<0.0001$). Within woody plants, the losses of deciduous shrubs were 14 times greater than
263 the losses of evergreen shrubs (5.20% vs. 0.37%; $t_{285.17}=5.38$, $p<0.0001$). Within herbaceous plants, the
264 losses of herbs were four times as large as the losses of graminoids (1.16% vs. 0.28%; $t_{121.15}=2.50$,
265 $p=0.0137$).

266 *Variation in herbivory among study sites*

267 At the site level, the CWBL due to invertebrate herbivores varied from 0.02% (Bogstranda, in Svalbard)
268 to 5.68% (Murmansk, Russia), with an average (\pm SE) of $0.94 \pm 0.31\%$ ($n=20$; **Figure 1**; **Online**
269 **Resource 3**). Aboveground biomass of vascular plants at our plots ranged from 2.56 to 854.68 g/m².
270 CWBL ranged between 0.002 and 10.68% across all plots examined, with an average (\pm SE) of $0.98 \pm$
271 0.17% ($n=92$).

272 Two models received similar support (Δ AICc <2 ; models 1 and 4 in **Table 3**). Both models included the
273 effect of long-term mean July temperature (**Table 3**); the second best model also included total
274 aboveground biomass, but its effect was not significantly different from zero ($estimate = -0.001$, 95% CI=
275 $(-0.002, 0)$; **Online Resource 4**). The models predicted a linear positive relationship between the log-
276 transformed community weighted biomass lost (CWBL) and July temperature (**Figure 2**), with an
277 estimated increase of 0.11% CWBL per 1 °C (model 1: $estimate = 0.106$, 95% CI= $(0.028, 0.184)$; model

278 4: *estimate*= 0.114, 95% *CI*= (0.038, 0.190)). However, the models still had a high percentage of
279 unexplained variability between the different tundra sites, associated with the random effect (model 1:
280 67.73%, model 4: 65.14%; **Online Resource 4**).

281

282 **Discussion**

283 Invertebrate herbivory was detected at all our 20 study sites, suggesting that it is a widespread
284 phenomenon throughout the tundra biome. However, the intensity of herbivory was generally low and
285 seemed to be influenced by summer temperature and other unknown local site characteristics.

286 At the community level, the mean foliar biomass lost to invertebrates was 0.94% (n=20), ranging from
287 0.02% to 5.69%. These levels are consistent with the average value of 0.56% reported from shrubs
288 growing in tundra regions of the European Arctic (Kozlov et al. 2015a) and with an estimate of 1.20%
289 loss calculated from the regressions of woody plant herbivory vs. latitude (after Kozlov et al. 2015b) for
290 the average latitude of our Arctic study sites (68.1 °N). Thus, we conclude that in tundra, plant foliar
291 losses to invertebrate herbivores at background (i.e., non-outbreak) levels are around 1% of foliar
292 biomass. This value is 5–13 times lower than reported in temperate plant communities. For example, in
293 temperate herbaceous communities, invertebrates reduced plant biomass by 13% (Coupe and Cahill
294 2003), and tissue loss due to invertebrates in temperate forests was 5–8% (Kozlov et al. 2015b). This
295 discrepancy may be partially attributed to the species-specific data used for the temperate studies
296 compared to the community-weighted method used in our study, or may simply reflect the lower levels of
297 invertebrate herbivory in the tundra (Kozlov et al. 2015a).

298 The variation in community weighted biomass lost to background invertebrate herbivory was associated
299 with long-term summer temperatures. Our sites spanned a range of summer (July) temperatures across the
300 tundra biome, from 2.9 to 14.8 °C. Warmer sites had significantly higher levels of invertebrate herbivory
301 despite a large variation among sites. Our model indicated a logarithmic relationship between long-term
302 July temperature and CWBL, suggesting that sites with higher temperatures have a more pronounced
303 increase in herbivory than cooler sites. As a first step to approximate the effects of future warming on
304 tundra invertebrate herbivory, we can adopt a space-for-time substitution approach to broadly infer
305 changes in herbivory from locations with different climatic variables (see for example Barrio et al. 2017).
306 Given the lack of long-term monitoring data on invertebrate herbivory in tundra and despite its
307 limitations, this approach provides the best solution and allows generating predictions that can then be
308 tested through monitoring or manipulative field experiments. According to our model, a single degree

309 increase in temperature will have a stronger effect on herbivory levels at higher temperatures (i.e. in the
310 low Arctic) compared with lower temperatures (i.e. in the high Arctic). For example, an increase in
311 temperature from 4°C to 5°C results in an increase in CWBL of 0.02%, while increasing from 13°C to
312 14°C results in an increase of 0.20%. Depending on the scenario, global temperatures are predicted to
313 increase by 1.1–2.9°C to 2.4–6.4°C over the next century, and this increase is expected to be more
314 pronounced in the Arctic (IPCC 2013; Overland et al. 2017). These predicted increases in temperature
315 would shift even our coldest sites (in Svalbard, Norway; 2.9 °C) into the temperature range where
316 herbivory levels begin to increase more rapidly (**Figure 2**). We also found that for sites with mean
317 temperatures <6 °C, there was very little variation in herbivory level – it was always very low and all
318 observations were clustered near the trend line. However, at sites with mean July temperatures >8 °C, the
319 intensity of herbivory becomes much more variable, with some sites showing low herbivory while others
320 had much higher levels. This suggests that a threshold may exist, below which invertebrate herbivory is
321 consistently low. Once this threshold is crossed at higher temperatures, herbivory can sometimes be very
322 high but other site-specific factor(s) may be constraining the levels of herbivory, resulting in the
323 variability observed in the present study (**Figure 2**). However, our assessment was based on a single year
324 and temporal variation may not be consistent across sites, highlighting the need for long-term monitoring
325 of invertebrate herbivory across multiple sites in tundra ecosystems.

326 Our models indicate that long-term mid-summer temperatures are partially responsible for this trend
327 rather than the climatic conditions in the year of sampling. This may be partially related to the life
328 histories of high latitude insects, which tend to have life cycles that span multiple years (Danks 1992).
329 Warmer summers year after year may thus have a greater effect than one single warm season, if, for
330 example, insects are able to complete their life cycle in fewer growing seasons, or if species are able to
331 complete multiple generations in a single summer. Further, long-term warming could allow lower-latitude
332 species (with shorter generation times, higher growth rates, and warmer temperature requirements) to
333 persist at higher latitudes. In contrast, other studies have found that weather in the year of sampling has a
334 stronger effect on herbivory than long-term climate data (Kozlov et al. 2013, Barrio et al. 2017). These
335 studies however, were investigating herbivory levels on a single or a few plant species rather than at the
336 community level. The number of plant species involved in studies estimating herbivore damage can affect
337 the inferences of these studies, with studies including fewer species tending to overestimate damage
338 (Zvereva and Kozlov 2019). Warming can also influence the feeding choices of invertebrate herbivores
339 (Barrio et al. 2016a, Gamarra et al. 2018), so patterns of herbivory of a single species may not be
340 representative of what happens at the community level. An alternative explanation could be simply that
341 the weather in the year of sampling in the present study might have been unusual. Most sites had a colder

342 (14 out of 20) and drier (16 out of 20) summer than their long-term average. Longer-term monitoring may
343 be able to capture the effects of interannual temperature variation on herbivory, and this could be
344 effectively implemented through coordinated efforts like the Circumpolar Biodiversity Monitoring
345 Programme (CBMP; e.g. Gillespie et al. 2019).

346 Our models including precipitation had little support in explaining the variation in background
347 invertebrate herbivory (**Table 3**), but this does not rule out an important role for precipitation as a
348 mediating factor in changing tundra environments (Bintanja and Andry 2017). Barrio et al. (2017) found a
349 positive effect of both temperature and precipitation when examining herbivory on dwarf birch (*B.*
350 *glandulosa-nana*) across the tundra biome. Again, this could be an indication that patterns at the species
351 level may not hold at the community level. Precipitation can influence invertebrate herbivory through its
352 effects on leaf toughness, yet at the community level this effect could be masked because the community
353 can be made up of plant species with varying levels of drought tolerance.

354 A large percentage of the variation in invertebrate herbivory however was not explained by the effect of
355 long-term mean summer temperature (i.e. the variance associated with the random effect of site was
356 67.73%). This suggests that local site characteristics other than temperature are driving differences in
357 herbivory between the sites, and emphasizes the usefulness of longitudinal studies, such as the present
358 one, to better explore the role of climate on biotic interactions at a biome-wide scale. This site-specificity
359 is consistent with recent studies that have found strong local effects in the structuring of Arctic arthropod
360 communities (Hansen et al. 2016). For example, local variation in shrub cover can influence the
361 composition of the arthropod community assemblage, through locally increasing habitat structural
362 complexity, such that higher shrub cover leads to a larger and more diverse community of arthropods
363 (Rich et al. 2013; Asmus et al. 2018). At a local scale, herbivory rates can also be influenced by nutrient
364 concentrations in the soil that influence leaf quality (Semenchuk et al. 2015). Higher nutrient
365 concentrations can lead to increased palatability of plant species, and ultimately higher levels of herbivory
366 (Torp et al. 2010a, b; Semenchuk et al. 2015). Presence of vertebrate herbivores may also affect the
367 intensity of invertebrate herbivory through their direct and indirect effects on the abundance of
368 invertebrate herbivores (Suominen et al. 1999, 2003).

369 Other local drivers, such as snow cover, can also contribute to small-scale heterogeneity in tundra
370 landscapes (Kankaanpää et al. 2018). Snow cover can vary substantially on a local scale due to variations
371 in topography (e.g. hollows with deep snow vs. windswept areas with little snow) (Torp et al. 2010a, b).
372 Variation in the duration of snow cover can influence overwinter protection of plants (Torp et al. 2010a)
373 and invertebrates (Danks 2004), timing of emergence for plants (Torp et al. 2010a) and invertebrates

374 (Høye and Forchhammer 2008), the level of nitrogen in the soil (Semenchuk et al. 2015) and
375 subsequently in leaf tissue (Torp et al. 2010a, b; Semenchuk et al. 2015), as well as the local composition
376 of arthropod communities in tundra (Kankaanpää et al. 2018). Accounting for the variation in these local
377 drivers and their effects on invertebrate herbivory would require site-specific measurements, but represent
378 a critical step to understand the variability in the observed patterns of herbivory.

379 Lastly, the structure and composition of plant communities may also influence invertebrate herbivory. In
380 general, different growth forms have differing leaf tissue palatability such that deciduous plants are more
381 palatable than evergreens (MacLean Jr. and Jensen 1985; Turcotte et al. 2014). Within this study, the 13
382 species that had >1% of their leaf area lost were deciduous shrubs (7 species), herbaceous species (4),
383 graminoids (1), and one palatable evergreen shrub (*Vaccinium vitis-idaea*). As well, deciduous shrubs had
384 an average of 5.20% of their leaf area consumed compared with 1.16% for herbs, 0.37% for evergreen
385 shrubs, and 0.28% for graminoids. This result supports our hypothesis that different plant functional
386 groups experience different levels of herbivory, with more palatable groups experiencing more damage.
387 These differences in the palatability of growth forms can translate into the differences observed between
388 sites. For example, we measured the highest levels of background herbivory in Murmansk, where a large
389 proportion (49.5%) of the focal species biomass corresponded to *V. myrtillus* and *B. nana*, both of which
390 are palatable deciduous shrubs (MacLean Jr. and Jensen 1985). In contrast, Theistareykir in Iceland had
391 one of the lowest levels of herbivory (0.06%) and two of the three focal species at this site were
392 unpalatable evergreen shrubs (*Empetrum nigrum* and *Calluna vulgaris*). In the long term, shifts in plant
393 community composition due to climate change – if more palatable plant species are favored – could
394 amplify the effects of warming on insect herbivory predicted by our model. In this sense, assessing
395 herbivory at the plant community level, while masking some of the individual species-specific responses,
396 may be more representative of a more diverse invertebrate herbivore community, and ultimately of
397 ecosystem responses to environmental changes.

398 **Conclusions**

399 Our study provides a first assessment of herbivory at the community level across the tundra biome,
400 providing a valuable baseline reference for evaluating future changes. Background invertebrate herbivory
401 in the tundra biome at the community level is low (the average loss of foliar biomass is 0.94%). Our study
402 suggests that plant losses to invertebrate herbivores in the tundra biome should increase, at least at some
403 sites, as the climate warms, even if some of these losses could be offset by increased plant biomass
404 production under warming (Day et al. 2008). Clarifying to what degree the relationship between climate
405 and invertebrate herbivory is a direct effect of warmer temperature, or an indirect effect of warming

406 temperatures on plant phenology, physiology, or abundance will help predict how the level of invertebrate
407 herbivory on tundra plants will change in response to a warmer climate. Our results also emphasize that
408 most of the variation in background invertebrate herbivory is associated with local site characteristics and
409 highlights knowledge gaps in our understanding of invertebrate herbivory in tundra. It is important
410 however, to keep in mind that our results represent a single-year snapshot: future studies should include
411 observations over longer periods of time to estimate year-to-year variation in the intensity of herbivory, as
412 temporal variation is also likely to play an important role. Ideally, future research should also include
413 characterizations of the invertebrate herbivore communities and their changes over time.

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435 **Compliance with Ethical Standards**

436 The authors declare that they have no conflict of interest.

437

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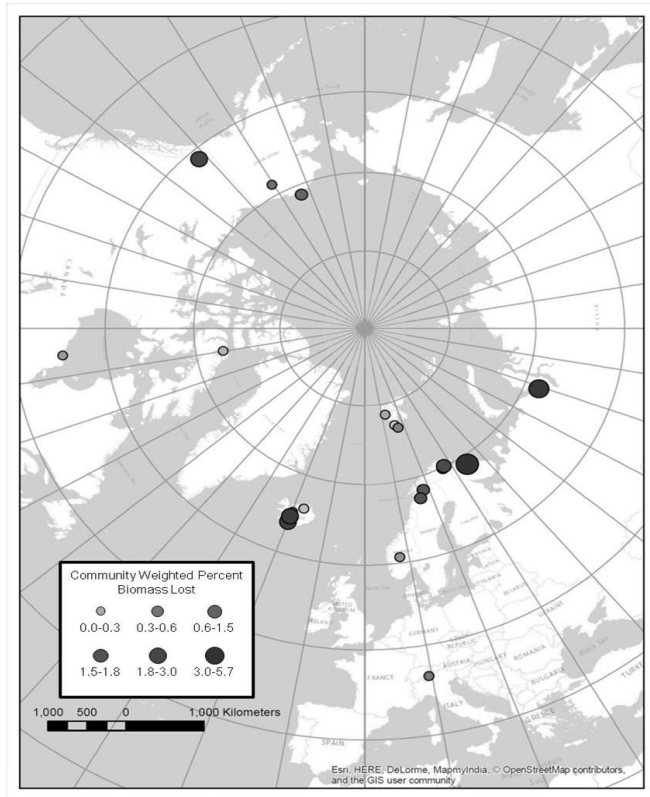
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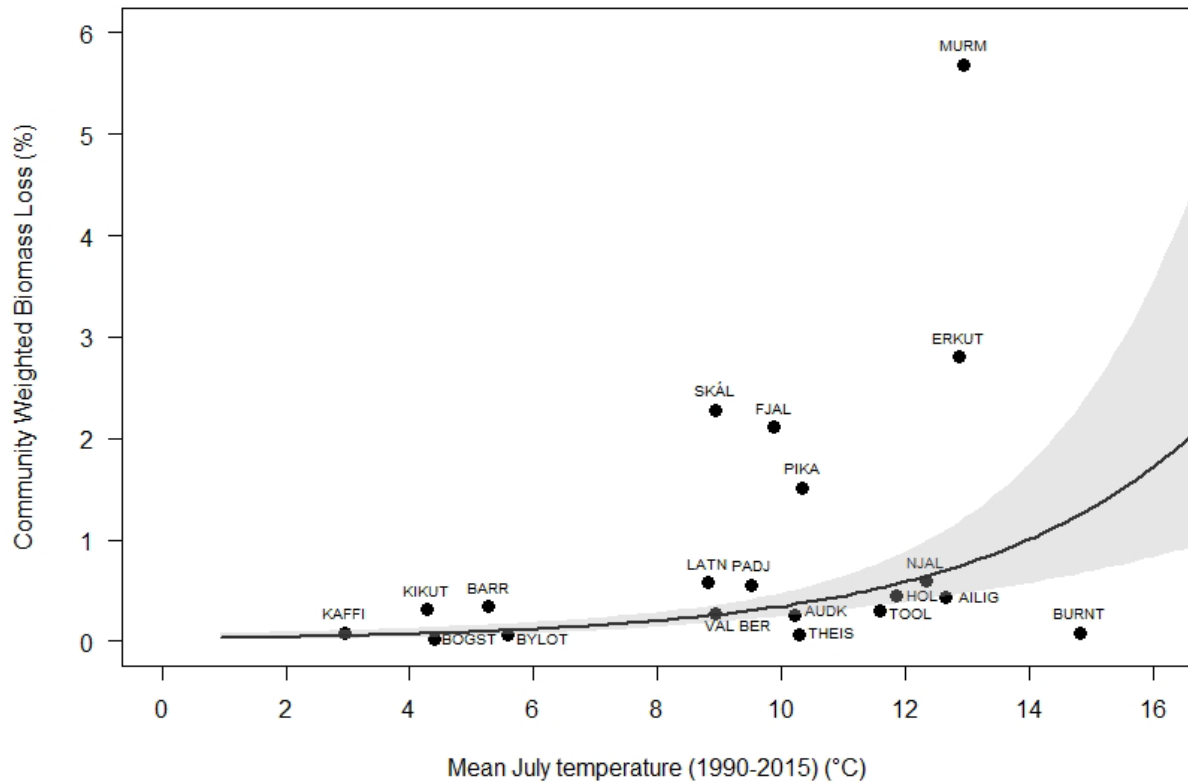
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624 **Fig. 1** Community weighted biomass lost (CWBL) to invertebrate herbivores at each of the 20 tundra sites. Size and
625 shade of dots indicate intensity of herbivory, grouped into 6 bins. Audkuluheidi (Iceland) and Ailigas (Finland) (see
626 Table 1) are covered by nearby sites, and belong in the 0.0-0.3 bin and 0.3-0.6 CWBL bins, respectively
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 629 **Fig 2** The relationship between the mean community weighted biomass lost (CWBL) to invertebrate herbivores and
 630 the mean long-term July temperature. Each point represents a study site (n=20); site names are indicated with
 631 abbreviations (see Table 1). The fitted line and 95% confidence interval (shaded) are shown. The point with the
 632 highest CWBL corresponds to Murmansk (MURM); running the analyses with and without this point did not change
 633 the overall trend
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655 **Table 1.** Description of the 20 study sites across the tundra biome: name abbreviation in capital letters and coordinates in decimal degrees are shown in brackets;
656 sampling date(s) in 2015, elevation, dominant habitat type (broad habitat types as defined by Walker et al. (2005); more specific CAVM sub-categories are
657 included in brackets when possible), number of plots sampled, identity of the focal species (and the number of plots in which each focal species was found at
658 each site) and climate variables: long-term average (1990-2015) and 2015 July temperature and precipitation (CRU data from Harris et al. (2014) for the nearest
659 grid cell with complete information). Sites with 2015 temperatures that differ by more than $\pm 1^\circ\text{C}$ from the long-term average are in bold, similarly sites that have
660 2015 precipitation levels that differ from the long-term mean by more than ± 10 mm are also in bold. Sites are listed geographically.

| Study Site | Region | Sampling Date(s) | Elevation (m a.s.l.) | Habitat Type | Number of Plots | Focal Species (number of plots present) | Mean July Temperature (1990-2015) ($^\circ\text{C}$) | Mean July Precipitation (1990-2015) (mm) | Mean July Temperature (2015) ($^\circ\text{C}$) | July Precipitation (2015) (mm) |
|---|---------|------------------|----------------------|-------------------------|-----------------|---|--|--|---|--------------------------------|
| Burntpoint Creek BURN (55.24, -84.32) | Canada | June 25 | 7-8 | Wetlands (W2) | 4 | <i>Carex aquatilis</i> (4), <i>Trichophorum cespitosum</i> (4), <i>Andromeda polifolia</i> (4) | 14.8 | 85.3 | 14.6 | 80.0 |
| Bylot Island BYLOT (73.15, -79.99) | Canada | July 16 | 44-102 | Graminoid (G2) | 5 | <i>Cassiope tetragona</i> (4), <i>Salix arctica</i> (5), <i>Arctagrostis latifolia</i> (4), <i>Oxyria digyna</i> (1), <i>Papaver radicatum</i> (1) | 5.6 | 36.6 | 7.5 | 18.0 |
| Pika Camp PIKA (61.22, -138.27) | Canada | July 27 | 1637-1774 | Prostrate-shrub (P1) | 5 | <i>Dryas octopetala</i> (5), <i>Salix arctica</i> (4), <i>Carex bigelowii</i> (5), <i>Salix reticulata</i> (1) | 10.3 | 58.0 | 10.5 | 80.4 |
| Ailigas AILIG (69.89, 27.07) | Finland | Aug 11-13 | 339-346 | Erect-shrub (S1) | 5 | <i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>Vaccinium vitis- idaea</i> (5) | 12.7 | 77.8 | 10.5 | 32.7 |
| Njallavaara NJAL (70.04, 27.60) | Finland | Aug 20-21 | 266-281 | Erect-shrub (S1) | 5 | <i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>V. vitis-idaea</i> (5) | 12.4 | 70.9 | 10.3 | 27.2 |
| Audkuluheidi AUDK (65.13, -19.67) | Iceland | Aug 4 | 479-498 | Prostrate-shrub (P1) | 5 | <i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>Silene acaulis</i> (2), <i>Vaccinium uliginosum</i> (3) | 10.2 | 48.5 | 8.4 | 40.5 |

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|--|----------|------------|-----------|----------------------|---|---|------|------|-------------|-------------|
| Fjallabak FJAL (63.83, -19.91) | Iceland | Aug 29 | 648-657 | Barren (B1) | 5 | <i>Salix herbacea</i> (5), <i>Armeria maritima</i> (4), <i>Cerastium alpinum</i> (1), <i>Salix arctica</i> (2), <i>O. digyna</i> (2) | 9.9 | 94.5 | 8.5 | 57.4 |
| Skálpanes SKÁL (64.52, -19.91) | Iceland | Aug 15 | 622-641 | Barren (B1) | 5 | <i>Salix herbacea</i> (5), <i>Silene acaulis</i> (5), <i>Juncus trifidus</i> (2), <i>Armeria maritima</i> (2), <i>Luzula spicata</i> (1) | 8.9 | 66.6 | 7.2 | 49.0 |
| Theistareykir THEIS (65.9, -17.08) | Iceland | Aug 2 | 326-341 | Prostrate-shrub (P1) | 5 | <i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>Calluna vulgaris</i> (5) | 10.3 | 54.8 | 7.9 | 76.7 |
| Hol HOL (60.70, 7.94) | Norway | July 17-20 | 1092-1147 | Erect-shrub (S2) | 4 | <i>Betula nana</i> (4), <i>Vaccinium myrtillus</i> (4), <i>V. uliginosum</i> (1), <i>Avenella flexuosa</i> (3) | 11.9 | 80.9 | 10.7 | 74.9 |
| Erkuta ERKUT (68.23, 69.15) | Russia | Aug 1-3 | 18 | Wetlands (W3) | 5 | <i>Betula nana</i> (5), <i>V. vitis-idea</i> (5), <i>Carex</i> sp. (5) | 12.9 | 41.0 | 11.2 | 60.1 |
| Murmansk MURM (68.87, 34.54) | Russia | Aug 11 | 246-265 | Erect-shrub (S1) | 5 | <i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>V. myrtillus</i> (5) | 13.0 | 69.3 | 10.3 | 46.6 |
| Bogstranda BOGST (77.02, 15.75) | Svalbard | July 18 | 20-37 | Prostrate-shrub (P1) | 5 | <i>Salix polaris</i> (5), <i>Saxifraga oppositifolia</i> (5), <i>Festuca rubra</i> (5) | 4.4 | 46.0 | 4.6 | 32.5 |
| Kaffiøyra KAFFI (78.60, 12.24) | Svalbard | July 14 | 27-31 | Prostrate-shrub (P1) | 5 | <i>D. octopetala</i> (3), <i>Salix polaris</i> (5), <i>Silene acaulis</i> (5), <i>Saxifraga oppositifolia</i> (1), <i>Bistorta vivipara</i> (1) | 2.9 | 53.1 | 3.6 | 56.0 |
| Kikutodden KIKUT (76.61, 16.96) | Svalbard | July 17 | 11-18 | Barren (B1) | 3 | <i>Luzula confusa</i> (3), <i>Cochlearia groenlandica</i> (1), <i>Poa arctica</i> (1), <i>Salix polaris</i> (1), <i>Saxifraga hyperborea</i> (1), <i>Cerastium arcticum</i> (2) | 4.3 | 48.2 | 4.3 | 35.0 |

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|--|-------------|---------|---------|---|---|--|------|-------|-------------|--------------|
| Latnjajaure LATN (68.21, 18.29) | Sweden | Aug 4 | 1000 | Erect-shrub (Low Arctic dwarf birch tundra*) | 1 | <i>Salix herbacea</i> (1), <i>Empetrum nigrum</i> (1), <i>Betula nana</i> (1) | 8.8 | 102.8 | 7.1 | 63.5 |
| Padjelanta PADJ (67.31, 16.69) | Sweden | Aug 2-3 | 580-641 | Erect-shrub (S2) | 5 | <i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>V. vitis-idaea</i> (3), <i>V. uliginosum</i> (2) | 9.5 | 106.4 | 7.8 | 85.3 |
| Val Bercla VAL BER (46.47, 9.58) | Switzerland | July 9 | 2490 | Alpine tundra* | 5 | <i>Primula integrifolia</i> (5), <i>Kalmia procumbens</i> (5), <i>Helictochloa versicolor</i> (5) | 8.9 | 229.0 | 12.1 | 104.4 |
| Barrow BARR (71.30, -156.67) | USA | Aug 7-8 | 10 | Wetlands (W1) | 5 | <i>Salix rotundifolia</i> (2), <i>Arctagrostis latifolia</i> (3), <i>Carex aquatilis</i> (5), <i>Salix pulchera</i> (3), <i>Petasites frigidus</i> (1), <i>V. vitis-idea</i> (1) | 5.3 | 21.8 | 5.1 | 5.8 |
| Toolik Lake TOOL (68.64, 149.57) | USA | Aug 1 | 730-746 | Graminoid (G4) | 5 | <i>Betula nana</i> (5), <i>Rhododendron tomentosum</i> (5), <i>V. vitis-idaea</i> (5), <i>Eriophorum vaginatum</i> (5), <i>Carex bigelowii</i> (5) | 11.6 | 45.0 | 11.4 | 38.6 |

661 *Virtanen et al. (2016)

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676 **Table 2.** List of all 42 focal vascular plant species, their growth form, total number of sites and plots they were found in, number of samples, total number of
677 leaves analyzed for each species, number of leaves with external damage, gall damage, and mining damage, number of total damaged leaves for each species, and
678 the corresponding average percent leaf area damaged (PLAD) for those samples. Some leaves experienced more than one type of herbivory and therefore the
679 total number of leaves damaged is less than the sum of the three damage types in some plant species. In total, 77,586 leaves were examined. Species taxonomy
680 follows Roskov et al. (2017).

| Focal Species | Growth Form | Study Sites | Plots | Samples | Leaves | External Damage | Gall Damage | Mine Damage | Total Damaged | Average PLAD (%) |
|--|-----------------|-------------|-------|---------|--------|-----------------|-------------|-------------|---------------|------------------|
| <i>Betula nana</i> L. | Deciduous shrub | 10 | 45 | 135 | 14779 | 2176 | 12 | 15 | 2176 | 2.08 |
| <i>Salix arctica</i> Pall. | Deciduous shrub | 3 | 11 | 23 | 2299 | 843 | 63 | 9 | 899 | 3.18 |
| <i>Salix herbacea</i> L. | Deciduous shrub | 3 | 11 | 33 | 3400 | 1007 | 3 | 10 | 1020 | 3.89 |
| <i>Salix polaris</i> Wahlenb. | Deciduous shrub | 3 | 11 | 33 | 3330 | 40 | 34 | 5 | 79 | 0.11 |
| <i>Salix pulchra</i> Cham. | Deciduous shrub | 1 | 3 | 3 | 293 | 8 | 2 | 0 | 10 | 0.03 |
| <i>Salix reticulata</i> L. | Deciduous shrub | 1 | 1 | 3 | 301 | 168 | 9 | 110 | 231 | 9.13 |
| <i>Salix rotundifolia</i> Trautv. | Deciduous shrub | 1 | 2 | 2 | 200 | 17 | 0 | 0 | 17 | 1.29 |
| <i>Vaccinium myrtillus</i> L. | Deciduous shrub | 2 | 9 | 27 | 2756 | 1334 | 13 | 59 | 1384 | 26.05 |
| <i>Vaccinium uliginosum</i> L. | Deciduous shrub | 3 | 6 | 18 | 1883 | 75 | 8 | 8 | 91 | 1.08 |
| <i>Andromeda polifolia</i> L. | Evergreen shrub | 1 | 4 | 12 | 1203 | 28 | 40 | 0 | 67 | 0.30 |
| <i>Calluna vulgaris</i> (L.) Hull | Evergreen shrub | 1 | 5 | 15 | 1500 | 1 | 0 | 0 | 1 | 0.01 |
| <i>Cassiope tetragona</i> (L.) D. Don | Evergreen shrub | 1 | 4 | 4 | 400 | 0 | 0 | 0 | 0 | 0 |
| <i>Dryas octopetala</i> L. | Evergreen shrub | 2 | 8 | 23 | 2308 | 212 | 3 | 3 | 216 | 0.78 |
| <i>Empetrum nigrum</i> L. | Evergreen shrub | 7 | 31 | 93 | 9368 | 70 | 1 | 0 | 71 | 0.16 |
| <i>Kalmia procumbens</i> (L.) Gift, Kron & P.F. Stevens ex Galasso, Banfi & F. Conti | Evergreen shrub | 1 | 5 | 5 | 500 | 9 | 13 | 0 | 22 | 0.25 |
| <i>Rhododendron tomentosum</i> Harmaja | Evergreen shrub | 1 | 5 | 15 | 1502 | 3 | 1 | 1 | 5 | 0.03 |
| <i>Vaccinium vitis-idaea</i> L. | Evergreen shrub | 6 | 25 | 69 | 6935 | 408 | 720 | 66 | 1181 | 1.46 |
| <i>Arctagrostis latifolia</i> (R. Br.) Griseb | Graminoid | 2 | 7 | 7 | 692 | 6 | 1 | 0 | 7 | 0.01 |
| <i>Avenella flexuosa</i> (L.) Drejer | Graminoid | 1 | 3 | 9 | 947 | 0 | 0 | 0 | 0 | 0 |
| <i>Carex aquatilis</i> Wahlenb. | Graminoid | 2 | 9 | 17 | 1666 | 33 | 0 | 57 | 90 | 0.11 |
| <i>Carex bigelowii</i> Torr. | Graminoid | 2 | 10 | 30 | 2955 | 191 | 0 | 21 | 211 | 0.76 |
| <i>Carex</i> spp. L. | Graminoid | 1 | 5 | 15 | 1471 | 143 | 0 | 283 | 407 | 0.93 |
| <i>Eriophorum vaginatum</i> L. | Graminoid | 1 | 5 | 15 | 1471 | 10 | 0 | 7 | 17 | 0.03 |

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|---|-----------|---|----|----|------|-----|----|----|-----|------|
| <i>Festuca rubra</i> L. | Graminoid | 1 | 5 | 15 | 1510 | 1 | 0 | 0 | 1 | 0 |
| <i>Helictochloa versicolor</i> (Vill.) Romero Zarco | Graminoid | 1 | 5 | 5 | 500 | 1 | 0 | 2 | 3 | 0.11 |
| <i>Juncus trifidus</i> L. | Graminoid | 1 | 2 | 6 | 600 | 0 | 0 | 0 | 0 | 0 |
| <i>Luzula confusa</i> Lindeberg | Graminoid | 1 | 3 | 9 | 904 | 74 | 0 | 0 | 74 | 1.65 |
| <i>Luzula spicata</i> (L.) DC. | Graminoid | 1 | 1 | 3 | 304 | 3 | 0 | 0 | 3 | 0.03 |
| <i>Poa arctica</i> R. Br. | Graminoid | 1 | 1 | 3 | 300 | 0 | 0 | 0 | 0 | 0 |
| <i>Trichophorum cespitosum</i> (L.) Hartm. | Graminoid | 1 | 5 | 12 | 1175 | 0 | 0 | 0 | 0 | 0 |
| <i>Armeria maritima</i> (Mill.) Willd | Herb | 2 | 6 | 18 | 1802 | 145 | 16 | 0 | 161 | 0.90 |
| <i>Bistorta vivipara</i> (L.) Delarbre | Herb | 1 | 1 | 3 | 195 | 10 | 0 | 1 | 11 | 0.33 |
| <i>Cerastium alpinum</i> L. | Herb | 1 | 1 | 3 | 299 | 4 | 0 | 7 | 11 | 1.57 |
| <i>Cerastium arcticum</i> Lange | Herb | 1 | 2 | 6 | 604 | 15 | 7 | 1 | 23 | 0.27 |
| <i>Cochlearia groenlandica</i> L. | Herb | 1 | 1 | 3 | 300 | 3 | 14 | 0 | 16 | 0.54 |
| <i>Oxyria digyna</i> (L.) Hill | Herb | 2 | 3 | 7 | 690 | 65 | 51 | 95 | 199 | 6.13 |
| <i>Papaver radicum</i> Rottb. | Herb | 1 | 1 | 1 | 97 | 0 | 0 | 10 | 10 | 0.73 |
| <i>Petasites frigidus</i> (L.) Fr. s.l. | Herb | 1 | 1 | 1 | 104 | 57 | 0 | 0 | 57 | 1.60 |
| <i>Primula integrifolia</i> L. | Herb | 1 | 5 | 5 | 437 | 35 | 0 | 2 | 37 | 1.36 |
| <i>Saxifraga hyperborea</i> R. Br. | Herb | 1 | 1 | 3 | 303 | 5 | 1 | 0 | 6 | 0.18 |
| <i>Saxifraga oppositifolia</i> L. | Herb | 2 | 6 | 17 | 1701 | 0 | 0 | 0 | 0 | 0 |
| <i>Silene acaulis</i> (L.) Jacq. | Herb | 3 | 12 | 36 | 3602 | 65 | 13 | 0 | 78 | 0.36 |

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694 **Table 3.** The five models used to explain the variation in community weighted biomass lost (CWBL) to invertebrate
 695 herbivory and the null model. Models were created using Linear Mixed Effects Models with site as a random effect.
 696 AICc values and weights are presented for comparison between models. LTMT = long-term mean temperature;
 697 LTMP = long-term mean precipitation; DT2015 = 2015 temperature difference; DP2015 = 2015 precipitation
 698 difference; TBM = total plant biomass; Habitat = site habitat type.

| Model | Predictors | df | AICc | AICc Weight |
|-------|------------------------|----|-------|-------------|
| Null | N/A | 3 | 142.3 | 0.06 |
| 1 | LTMT | 4 | 138.5 | 0.38 |
| 2 | LTMT + LTMP | 5 | 140.8 | 0.13 |
| 3 | LTMT + DT2015 + DP2015 | 6 | 140.8 | 0.13 |
| 4 | LTMT + TBM | 5 | 139.6 | 0.23 |
| 5 | LTMT + Habitat | 9 | 141.5 | 0.09 |

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