

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

3 Sarah I RHEUBOTTOM<sup>1\*</sup>, Isabel C BARRIO<sup>2,3</sup>, Mikhail V KOZLOV<sup>4</sup>, Juha M ALATALO<sup>5,6</sup>, Tommi  
4 ANDERSSON<sup>7</sup>, Ashley L ASMUS<sup>8,9</sup>, Capucine BAUBIN<sup>10</sup>, Francis Q BREARLEY<sup>11</sup>, Dagmar D  
5 EGELKRAUT<sup>12,13</sup>, Dorothee EHRICH<sup>10</sup>, Gilles GAUTHIER<sup>14</sup>, Ingibjörg Svala JÓNSDÓTTIR<sup>3,15</sup>, Sophia  
6 KONIECZKA<sup>16</sup>, Esther LÉVESQUE<sup>17</sup>, Johan OLOFSSON<sup>18</sup>, Janet S PREVÉY<sup>19,20</sup>, Guillaume  
7 SLEVAN-TREMBLAY<sup>14</sup>, Aleksandr SOKOLOV<sup>21,22</sup>, Natalia SOKOLOVA<sup>21,22</sup>, Svetlana  
8 SOKOVNINA<sup>23</sup>, James D M SPEED<sup>24</sup>, Otso SUOMINEN<sup>7</sup>, Vitali ZVEREV<sup>4</sup>, David S HIK<sup>1,25</sup>

9 <sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, Canada T6G 2E9

10 <sup>2</sup>Agricultural University of Iceland Árleyni 22, Keldnaholt, IS-112 Reykjavík, Iceland

11 <sup>3</sup>Institute of Life and Environmental Sciences, University of Iceland, Sturlugata 7, IS-101 Reykjavík, Iceland

12 <sup>4</sup>Section of Ecology, Department of Biology, University of Turku, FI-20014, Turku, Finland

13 <sup>5</sup>Department of Biological and Environmental Sciences, College of Arts and Sciences, Qatar University, P.O. Box 2713, Doha,  
14 Qatar

15 <sup>6</sup>Environmental Science Center, Qatar University, PO Box 2713, Doha, Qatar

16 <sup>7</sup>Kevo Subarctic Research Institute, Biodiversity Unit, University of Turku, FI-20014, Turku, Finland

17 <sup>8</sup>Department of Biology, University of Texas at Arlington, Arlington, Texas USA

18 <sup>9</sup>Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, Minnesota, USA

19 <sup>10</sup>Department of Arctic and Marine Biology, University of Tromsø, Tromsø, Norway

20 <sup>11</sup>School of Science and the Environment, Manchester Metropolitan University, Chester Street, Manchester, M1 5GD, UK

21 <sup>12</sup>Department of Ecology and Environmental Science, Umeå University, 901 87 Umeå, Sweden

22 <sup>13</sup>Department of Biology, University of Bergen, Norway (*current address*)

23 <sup>14</sup>Department of Biology and Centre d'études nordiques, Université Laval, 1045 Avenue de la Médecine, Quebec, QC G1V 0A6,  
24 Canada

25 <sup>15</sup>The University Centre in Svalbard, 9171 Longyearbyen, Norway

26 <sup>16</sup>Wildlife Research and Monitoring Section, Science and Research Branch, Ministry of Natural Resources, Ontario, Canada K9L  
27 1Z8

28 <sup>17</sup>Département des Sciences de l'environnement and Centre d'études nordiques, Université du Québec à Trois-Rivières, 3351  
29 Boul. des Forges, Trois-Rivières, QC G9A 5H7, Canada

30 <sup>18</sup>Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden

31 <sup>19</sup>Pacific Northwest Research Station, USDA-Forest Service, 3625 93rd Avenue SW, Olympia, Washington 98512

32 <sup>20</sup>WSL Institute for Snow and Avalanche Research SLF, Davos, Switzerland

33 <sup>21</sup>Arctic Research Station of Institute of plant and animal ecology, Ural branch, Russian academy of sciences, 629400, Zelenaya  
34 Gorka Str., 21, Labytnangi, Russia

35 <sup>22</sup>Arctic Research Center of Yamal-Nenets autonomous district, 129008, Respubliki Str., 20, Salekhard, Russia

36 <sup>23</sup>Institute of plant and animal ecology, Ural branch, Russian academy of sciences, 620144, 8 March Str, 202, Yekaterinburg,  
37 Russia

38 <sup>24</sup>Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, NO-7491  
39 Trondheim, Norway

40 <sup>25</sup>Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada

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42 \*corresponding author: Sarah I Rheubottom, email: [srheubot@ualberta.ca](mailto:srheubot@ualberta.ca); ORCID 0000-0001-9757-6652

43 ORCID of authors

Sarah I Rheubottom (0000-0001-9757-6652)
Isabel C Barrio (0000-0002-8120-5248)
Mikhail V Kozlov (0000-0002-9500-4244)
Juha M Alatalo (0000-0001-5084-850X)
Ashley L Asmus (0000-0001-5505-1372)
Dagmar D Egelkraut (0000-0002-2644-2144)
Dorothee Ehrich (0000-0002-3028-9488)
Gilles Gauthier (0000-0002-2624-3508)
Ingibjörg Svala Jónsdóttir (0000-0003-3804-7077)
Aleksandr Sokolov (0000-0002-1521-3856)
Natalia Sokolova (0000-0002-6692-4375)
James D M Speed (0000-0002-0633-5595)
Otso Suominen (0000-0002-7209-6078)
David S Hik (0000-0002-8994-9305)

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 km<sup>2</sup> 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 m<sup>2</sup>, 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 log<sub>10</sub>-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/m<sup>2</sup>.  
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 ( $\Delta$ 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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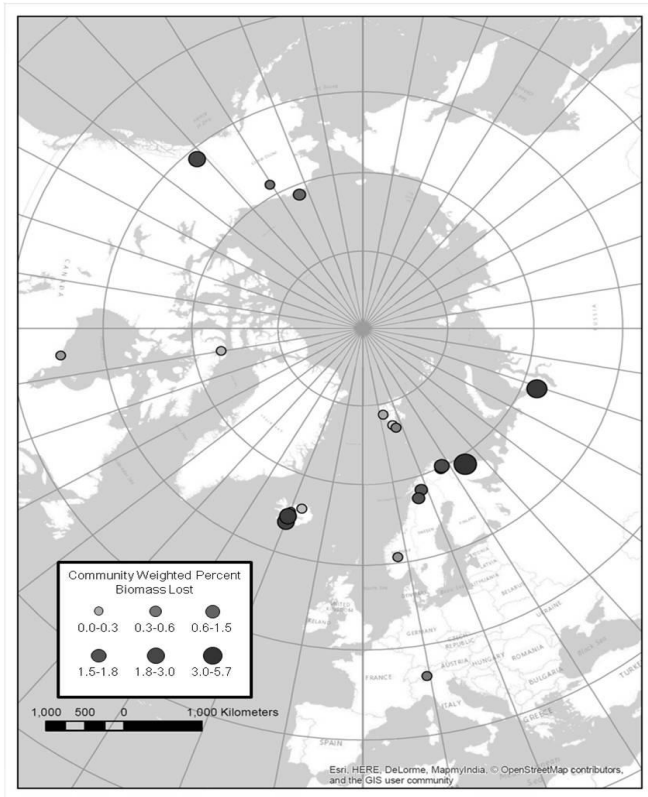
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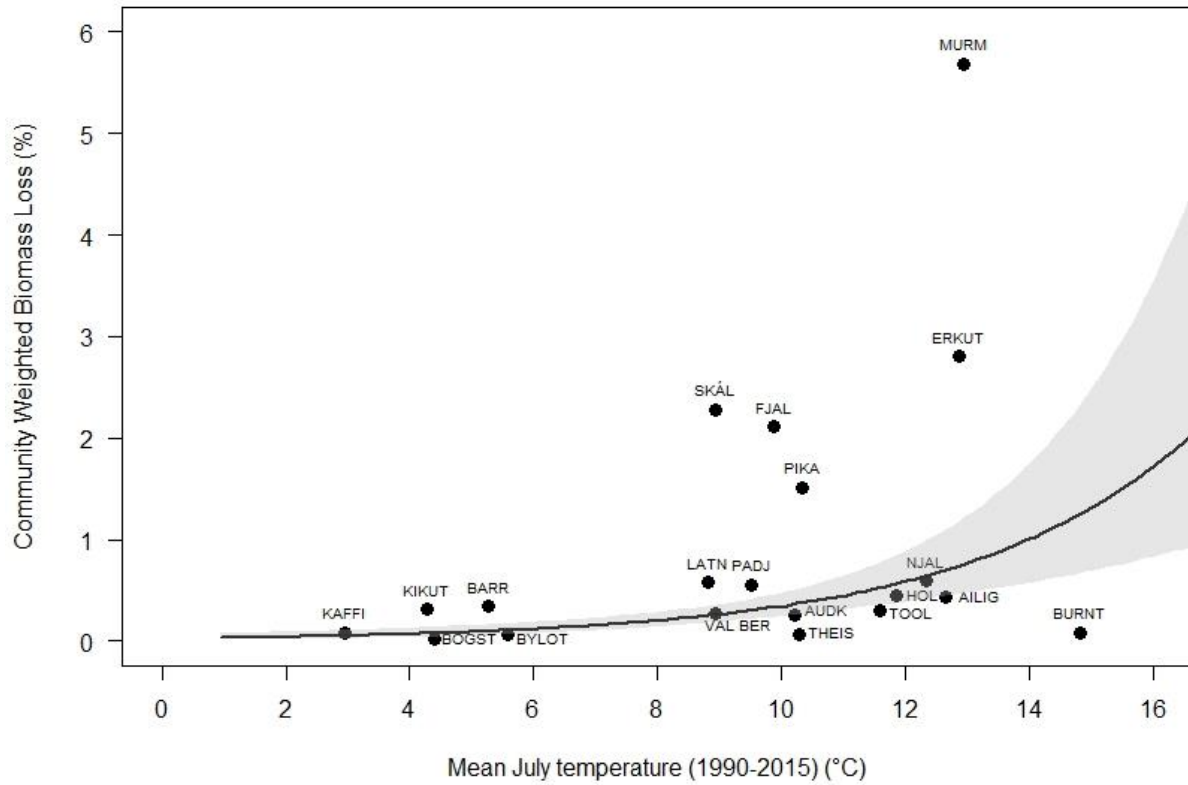
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624 **Fig. 1** Community weighted biomass lost (CWBL) to invertebrate herbivores at each of the 20 tundra sites. Size and  
625 shade of dots indicate intensity of herbivory, grouped into 6 bins. Audkuluheidi (Iceland) and Ailigas (Finland) (see  
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  $\pm 10$  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	<b>7.5</b>	<b>18.0</b>
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	<b>80.4</b>
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	<b>10.5</b>	<b>32.7</b>
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	<b>10.3</b>	<b>27.2</b>
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	<b>8.4</b>	40.5

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	<b>8.5</b>	<b>57.4</b>
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	<b>7.2</b>	<b>49.0</b>
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	<b>7.9</b>	<b>76.7</b>
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	<b>10.7</b>	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	<b>11.2</b>	<b>60.1</b>
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	<b>10.3</b>	<b>46.6</b>
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	<b>32.5</b>
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	<b>35.0</b>

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	<b>7.1</b>	<b>63.5</b>
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	<b>7.8</b>	<b>85.3</b>
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	<b>12.1</b>	<b>104.4</b>
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	<b>5.8</b>
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

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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



<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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