

1       **Background invertebrate herbivory on dwarf birch (*Betula glandulosa-nana***  
2 **complex) increases with temperature and precipitation across the tundra biome**

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## 74 **ABSTRACT**

75 Chronic, low intensity herbivory by invertebrates, termed background herbivory, has been understudied in tundra,  
76 yet its impacts are likely to increase in a warmer Arctic. The magnitude of these changes is however hard to  
77 predict as we know little about what drives current levels of invertebrate herbivory in tundra. We assessed the  
78 intensity of invertebrate herbivory on a common tundra plant, the dwarf birch (*Betula glandulosa-nana* complex),  
79 and investigated its relationship to latitude and climate across the tundra biome. Leaves from 187 sites at 55  
80 locations were inspected for signs of leaf damage by defoliating, mining and gall-forming invertebrates. Our  
81 results indicate that invertebrate herbivory is nearly ubiquitous across the tundra biome but occurs at low  
82 intensity. On average, invertebrates damaged 11.2% of the leaves and removed 1.4% of total leaf area. The  
83 damage was mainly caused by external leaf feeders, and most damaged leaves were only slightly affected (12%  
84 leaf area lost). Foliar damage was consistently positively correlated with summer temperature and, to a lesser  
85 extent, precipitation in the year of data collection, irrespective of latitude. Our models predict that, on average,  
86 foliar losses to invertebrates on dwarf birch are likely to increase by 6-7% over the current levels with a 1 °C  
87 increase in summer temperatures. Our results show that invertebrate herbivory on this common tundra shrub is  
88 small in magnitude but given its prevalence and dependence on climatic variables, background invertebrate  
89 herbivory should be included in predictions of climate change impacts on tundra ecosystems.

90 **Keywords:** background insect herbivory, climate change, externally-feeding defoliators, latitudinal herbivory  
91 hypothesis, leaf damage, leaf miners, gall-makers, macroecological pattern

## 92 INTRODUCTION

93 The role of invertebrate herbivores in tundra ecosystems has been understudied (Haukioja 1981). Admittedly, the  
94 proportion of herbivore taxa among invertebrates is lower in Arctic regions than at lower latitudes (Danks 1986),  
95 and invertebrate herbivores generally occur at relatively low abundances (Haukioja 1981). However, outbreaks of  
96 invertebrate herbivores have been well documented in the forest-tundra ecotone (Jepsen et al. 2008, Kaukonen et  
97 al. 2013) and occasionally in tundra (Post and Pedersen 2008). These massive defoliation events have large  
98 impacts on subarctic birch forests, enhancing resource turnover through deposition of frass and carcasses to the  
99 soil (Kaukonen et al. 2013) and causing vegetation shifts from forested to open conditions with consequences for  
100 ecosystem functioning and trophic interactions (Jepsen et al. 2013, Olofsson et al. 2013, Parker et al. 2016). In  
101 contrast, chronic leaf consumption by invertebrate herbivores when they occur at low densities, termed  
102 background herbivory (Kozlov and Zvereva 2017), has long been assumed to be unimportant, especially in the  
103 Arctic (Batzli et al. 1980, Haukioja 1981). However, recent studies in boreal forest indicate that chronic  
104 invertebrate herbivory can have stronger impacts on plant growth in the long term than infrequent bouts of severe  
105 damage (Zvereva et al. 2012), and can play a major role in ecosystem-level nutrient cycling (Metcalfe et al. 2016).  
106 Yet, the extent, drivers and consequences of background herbivory across the tundra biome remain unquantified  
107 (Kozlov et al. 2015a).

108 The latitudinal herbivory hypothesis suggests that the intensity of herbivory should decrease with increasing  
109 latitude (Coley and Barone 1996). In its original formulation, it was argued that a wider diversity of specialist  
110 herbivores in tropical areas would lead to increased herbivory rates. Empirical evidence has found support for this  
111 hypothesis at the global scale, demonstrating that invertebrate herbivory of woody plants is generally lower in the  
112 polar regions than in temperate and tropical zones (Kozlov et al. 2015b). However, the generality of the latitudinal  
113 herbivory hypothesis across plant functional types, insect species and spatial scales is still debated (Moles et al.  
114 2011, Anstett et al. 2016, Zhang et al. 2016). Latitudinal patterns in herbivory have been described for some  
115 species of plants and groups of insect herbivores (Pennings et al. 2009, Kozlov et al. 2015b, Moreira et al. 2015) but  
116 not others (Andrew and Hughes 2005, Kozlov 2008, Kozlov et al. 2016). Moreover, such studies have typically been  
117 conducted in temperate regions; whether such patterns can be found within the tundra biome remains unknown.  
118 Similarly, the mechanisms behind these macroecological patterns in background herbivory are poorly understood.  
119 Biotic and abiotic factors vary with latitude and this variability may promote variation in herbivory. For example, it  
120 has been suggested that, along with direct effects of climate, latitudinal gradients in herbivory may be shaped by  
121 changes in plant defensive chemistry (Moles et al. 2011), in predator pressure (Björkman et al. 2011) or by  
122 variations in leaf toughness (Onoda et al. 2011).

123 Climatic variables are usually considered one of the main drivers of latitudinal patterns in the intensity of biotic  
124 interactions. Temperature directly affects the performance and abundance of invertebrate herbivores (Bale et al.

125 2002), since the physiology and population dynamics of insects living at higher latitudes are generally controlled by  
126 temperature (Hodkinson and Bird 1998). Temperature could also affect invertebrate herbivores indirectly, through  
127 changes in the palatability or availability of their host plants (Bale et al. 2002). Warmer temperatures have been  
128 associated with increased levels of herbivory in the fossil record (Wilf and Labandeira 1999, Wilf et al. 2001) and in  
129 experimental field studies (Richardson et al. 2002, Roy et al. 2004). Temperature was also found to explain  
130 latitudinal patterns in background herbivory in northern boreal forests (Kozlov 2008), as well as annual variations  
131 in this pattern (Kozlov et al. 2013), with higher temperatures associated with increased levels of herbivory. The  
132 effects of precipitation on the levels and types of invertebrate herbivory have been studied less systematically  
133 (Bale et al. 2002). Temperature was found to be a better predictor of herbivory than precipitation at a global scale  
134 (Kozlov et al. 2015b, Zhang et al. 2016), yet precipitation has a stronger influence on the global patterns of leaf  
135 traits related to resistance to damage, with more resistant leaves in sites with lower annual precipitation (Onoda  
136 et al. 2011). Broad gradients of temperature and precipitation exist across the tundra biome; we therefore  
137 hypothesize that patterns of invertebrate herbivory will also be influenced by climatic gradients in this region.

138 Patterns of herbivory and their underlying mechanisms may also differ between feeding guilds of herbivores with  
139 contrasting life history traits (Hiura and Nakamura 2013, Anstett et al. 2014). Some studies have found that  
140 geographical patterns of different herbivores were driven by different climatic variables, suggesting that variation  
141 in the sensitivity of feeding guilds to climate could lead to disparate predictions under climate change (Leckey et al.  
142 2014, Moreira et al. 2015). For example, externally feeding defoliators are more exposed to abiotic variables and  
143 may respond to them directly, whereas internally feeding herbivores like leaf miners and gallers may be affected  
144 by abiotic variables indirectly through their effects on leaf traits (e.g. Andrew and Hughes 2005, Sinclair and  
145 Hughes 2008). For instance, precipitation affects the intensity of herbivory by leaf miners and gall-makers (Leckey  
146 et al. 2014), possibly through its effects on leaf toughness (Onoda et al. 2011). Tougher leaves are well defended  
147 against external herbivores but may favour internally feeding herbivores as they provide safer shelter against  
148 pathogens and reduce levels of desiccation (Carneiro et al. 2005). We propose that the same distinction between  
149 external and internal feeders will drive differences in the patterns of invertebrate herbivory in tundra.

150 Temperatures and precipitation are predicted to continue increasing in the Arctic (Cook et al. 2014), and warming  
151 is expected to occur at a higher rate than the global average (IPCC 2013). The rapid pace of environmental changes  
152 in the Arctic underscores the urgency of studying the responses of fundamental ecological processes, such as  
153 herbivory, to varying climatic conditions. Insects living at higher latitudes are highly responsive to climate changes  
154 (Hodkinson and Bird 1998), and warming-induced increases in insect herbivory are expected to be stronger at  
155 higher latitudes (Wolf et al. 2008, Kozlov et al. 2015b). Experimental studies in tundra have shown that the  
156 intensity of invertebrate herbivory increases with warming (Barrio et al. 2016, Birkemoe et al. 2016), but the lack  
157 of knowledge on current levels of background herbivory across the tundra biome constrains any meaningful  
158 predictions.

159 The objective of this study is to assess the intensity of background invertebrate herbivory and characterise its  
160 relationships with latitude and climatic variables in tundra. To achieve this goal, we measured leaf damage by  
161 tissue-feeding invertebrate herbivores on a common tundra plant with a circumpolar distribution, the dwarf birch  
162 (*Betula glandulosa-nana* complex), across a large number of sites spanning nearly 24° of latitude. Dwarf birch is a  
163 main food plant of many tundra herbivores (Koponen 1984, Bryant et al. 2014) and it is an important component in  
164 many shrub tundra plant communities. The wide distribution of dwarf birch facilitates comparisons within a single  
165 host plant across a latitudinal gradient (Anstett et al. 2016); further, the range and abundance of dwarf birch are  
166 predicted to expand in response to warming (Euskirchen et al. 2009, Myers-Smith et al. 2011). We test the  
167 following hypotheses: (i) background invertebrate herbivory is greatest at lower latitudes, consistent with the  
168 latitudinal herbivory hypothesis, or where summer temperature and precipitation are highest; and (ii) the patterns  
169 of invertebrate herbivory by different feeding guilds will correspond with different climatic variables, given their  
170 sensitivity to different environmental cues. Specifically, we expect leaf damage by externally-feeding defoliators to  
171 be more strongly associated with summer temperature than damage by internally feeding herbivores (leaf miners  
172 and galls), and conversely that the latter will be more affected by climatic variables that determine leaf  
173 toughness, such as precipitation.

174

## 175 **METHODS**

### 176 *Focal plant species and leaf sampling*

177 Dwarf birch is a taxonomic complex with several closely related and hybridizing species. The main taxonomic units  
178 that we identified are *Betula glandulosa* Michx., *B. nana* subsp. *nana* L. and *B. nana* subsp. *exilis* (Sukaczew) Hultén.  
179 Species identification was conducted by collectors in the field and verified based on distribution maps (**Figure 1**;  
180 Bryant et al. 2014). *Betula glandulosa* is distributed throughout the northern regions of North America, from  
181 Alaska to Newfoundland, as well as the southern part of Greenland (Feilberg 1984). *Betula nana* is distributed  
182 throughout the Arctic regions of Eurasia and North America, with *B. nana* subsp. *nana* occurring from Greenland  
183 through northern Europe to Western Siberia, and *B. nana* subsp. *exilis* occurring from Eastern Siberia to Alaska and  
184 into northern Canada (Bryant et al. 2014). These three taxonomic units differ in leaf chemistry: *B. nana* subsp.  
185 *exilis* and *B. glandulosa* have higher concentrations of phenolic glycosides, condensed tannins, and triterpenes,  
186 have lower leaf nitrogen, and are less palatable to vertebrate herbivores than *B. nana* subsp. *nana* (Bryant et al.  
187 2014, DeAngelis et al. 2015). However, the importance of these chemical differences for invertebrate herbivory is  
188 not known.

189 Plant material was collected in the summers of 2008-2013 (summarized by Kozlov et al. 2015b), 2014 and 2015  
190 between June 12 and September 17. Although different protocols were followed in different years, samples were

191 collected in a way that allowed for spatial comparisons to evaluate background herbivory and its relationship to  
192 abiotic conditions. The protocol used in 2008-2013 (see Appendix S2 to Kozlov et al. 2015b) aimed at sampling  
193 plant foliage for measurements of insect herbivory at the global scale. The 2014 protocol was designed to assess  
194 defensive chemistry of dwarf birches across the Arctic, irrespective of invertebrate herbivory (**Appendix S1**) and  
195 was slightly modified for the purpose of this study; we used only the first of two samples collected in 2014,  
196 consisting of top shoots (both long and short shoots), and disregarded the second sample (approx. 500 leaves)  
197 because it collected leaves from short shoots (primary growth) and therefore may not be representative of  
198 herbivory on the whole plant. The 2015 protocol was specifically aimed at measuring background invertebrate  
199 herbivory in tundra at the plant community level  
200 ([http://herbivory.biology.ualberta.ca/files/2016/11/background\\_herbivory\\_tundra.pdf](http://herbivory.biology.ualberta.ca/files/2016/11/background_herbivory_tundra.pdf)); here we report only the  
201 results for dwarf birch.

202 Briefly, all sampling protocols requested collection of birch leaves from several individuals per site (2-5 individuals  
203 were sampled in 2008-2013, 10 individuals in 2014, and 3 individuals in 2015). The samples included 71-500 leaves  
204 per site, where sites were defined as circular areas of approximately 10 m radius, at least 100 m apart. The  
205 number of sites within a location (i.e. spatially distinct 'study areas', at least 10 km apart) varied between 1 and 16  
206 (for the 2008-2013 and 2014 protocols, a minimum of 1 site per location was requested, while for the 2015  
207 protocol, the minimum number of sites per location was 5). Samples were collected from 187 sites in 55 locations,  
208 spanning 23.7° of latitude across the tundra biome (including non-Arctic locations in alpine areas), from 55.2° N to  
209 78.9° N (**Figure 1; Appendix S2**). The geographical distribution of locations was not designed in advance: the  
210 requests for sampling were distributed across the research community, and all samples received were included in  
211 our study.

### 212 *Leaf damage assessment*

213 Each leaf was inspected on both sides for leaf damage with a light source against the leaf to detect damage on the  
214 surface, and then with the light through the leaf, to detect damage inside the leaf. We distinguished damage  
215 caused by three different feeding guilds of invertebrate herbivores: external leaf feeders (chewing or  
216 skeletonization), and internally feeding miners and gall makers (**Appendix S3**). External feeding damage on dwarf  
217 birch is caused primarily by sawflies (Hymenoptera: Tenthredinidae) and by moth larvae (Lepidoptera) (Koponen  
218 1984). Leaf miners can include larvae of Lepidoptera and Coleoptera (Viramo 1962), whereas galls are formed by  
219 insects and eriophyid mites. Other herbivores, such as phloem-feeders, also occur on dwarf birch (Koponen 1984),  
220 but damage imposed by these insects could not be measured from leaf samples.

221

222 Each leaf was assigned to a damage class according to the main type of damage (multiple damage types on the  
223 same leaf occurred in less than 1% of leaves analysed) and to the visually estimated percentage of the leaf area  
224 damaged by invertebrates: intact leaves, 0.01-1, 1-5, 5-25, 25-50, 50-75 and 75-100% (Kozlov 2008). Samples from  
225 the three protocols were evaluated by three scorers (2008-2013 protocol by MKV, 2014 by EL, 2015 by ICB);  
226 assessments made by the three scorers on 6-10 training samples (100 leaves each) indicated no statistically  
227 significant effect of the scorer on the estimates of foliar damage (pairwise t-test: all  $p > 0.1$ ; intra-class correlation  
228 coefficients ranged between 0.56 and 0.88).

### 229 *Data analysis*

230 The intensity of invertebrate herbivory at each site was calculated using three complementary measures: 1)  
231 percentage of leaves damaged: the percentage of leaves that showed signs of invertebrate herbivory at a site; 2)  
232 percentage of leaf area damaged: the percentage of leaf area consumed or otherwise damaged by invertebrate  
233 herbivores over the total number of leaves inspected in a sample; and 3) average damage per damaged leaf: the  
234 average leaf area lost to invertebrate herbivores per damaged leaf. The percentage of leaves damaged indicates  
235 the distribution of damage within a site; the percentage of leaf area damaged gives an approximation of foliar loss  
236 per site as a measure of herbivory; and the average damage per damaged leaf reflects how much of the leaf area is  
237 affected, once a leaf is damaged (Kozlov 2008, Kozlov et al. 2015a). To calculate the latter two variables, the  
238 number of leaves in each damage class was multiplied by the corresponding median value of damage (i.e. 0 for  
239 intact leaves, 0.5% for the 0.01-1% class, 3% for the 1-5% class, 15% for the 5-25% class, 37.5% for the 25-50%  
240 class, 62.5% for the 50-75% class, and 87.5% for the 75-100% class) and summed for all damage classes. These  
241 values were divided by the total number of leaves to obtain an estimate of the percentage of total leaf area  
242 damaged, and by the number of damaged leaves to obtain the average damage per damaged leaf (Kozlov et al.  
243 2015a, b). All variables were calculated for all invertebrate herbivores and for the three different feeding guilds  
244 separately (**Appendix S4**); given the low occurrence of mines and galls, only the percentage of leaves damaged was  
245 included in the models for these groups.

246 To investigate the effects of latitude and climatic variables on invertebrate herbivory in tundra we built Linear  
247 Mixed Effects Models (LMM) for total herbivory and for each feeding group separately. In all models, sampling  
248 protocol (2008-2013, 2014 or 2015) was included as a random effect to account for potential confounding effects  
249 of year of sampling, person scoring leaf damage and/or protocol design. Nearly half of the locations (21 out of 55)  
250 sampled one site only so location could not be included in the models as a random factor; therefore,  
251 measurements of invertebrate herbivory for locations with more than one site were averaged across sites, and the  
252 number of sites sampled at each location was included as weights in the models to account for differences in  
253 sampling effort.

254 Climate variables were extracted from the Global Historical Climatology Network-Monthly (GHCN-M v3.2.1,  
255 Lawrimore et al. 2011). This dataset provides monthly mean temperatures and precipitation as a spatial raster (0.5  
256 degree resolution) based on weather station data. We extracted July temperature and precipitation for the year of  
257 sample collection, because current-season weather is more relevant to invertebrate herbivory than multi-year  
258 averages (Kozlov et al. 2013). Climate variables and latitude were included as predictors in the models.  
259 Correlations between continuous predictor variables were low ( $r < 0.4$ ; **Appendix S4**) and Variance Inflation Factors  
260 indicated no strong multicollinearity ( $VIF < 1.2$ ), so all three variables were included simultaneously in the models.  
261 Dwarf birch exhibits patterns of regional and taxonomic variation in defense against browsing by vertebrates  
262 (Bryant et al. 2014) that may also affect the observed patterns of invertebrate herbivory, so we included dwarf  
263 birch taxon (*B. glandulosa*, *B. nana* subsp. *exilis* and *B. nana* subsp. *nana*) as a fixed-effect variable in our analyses.  
264 We also included collection date, measured as day-of-year, as a fixed covariate in the models because foliar  
265 damage accumulates over the growing season, but damaged leaves tend to abscise prematurely (Torp et al. 2010,  
266 Kozlov et al. 2016). For the two locations where no invertebrate leaf damage was detected (Svalbard and Beringa  
267 Island), we assigned the lowest possible value for herbivory (0.1% for the percentage of leaves damaged by all  
268 herbivores and defoliators, 0.01% in the case of leaf miners and gallers, and 0.01% for leaf area damaged). The  
269 percentage of damaged leaves and the percentage leaf area affected by herbivory were then log-transformed to  
270 comply with model assumptions, which were checked by visually inspecting model residuals (Zuur et al. 2009). All  
271 analyses were run in R 3.2.3 (R Development Core Team 2015) using the *lme4* package to build LMMs (Bates et al.  
272 2015).

273

## 274 **RESULTS**

275 Feeding marks of invertebrate herbivores were found on 3,708 of the 29,308 leaves examined (12.7%). Damage by  
276 invertebrate herbivores affected between 0 and 46.0% of leaves at each location (mean  $\pm$  SE:  $11.2 \pm 1.3\%$ ; median=  
277 8.7%,  $n=61$ ). On average,  $1.4 \pm 0.2\%$  of leaf area was damaged at each location (median = 1.1%), and most  
278 damaged leaves were only slightly affected ( $12.1 \pm 1.0\%$  of leaf area damaged; median = 11.9%). The vast majority  
279 of damage (95.0%) was caused by defoliators. Damage by internally feeding herbivores (leaf miners and gallers)  
280 was found on relatively few leaves: 160 were mined by larvae of several moth species (see **Appendix S5** for  
281 identification of mines from 2015) and only 24 bore galls.

### 282 *Total herbivory*

283 Both the percentage of leaves with signs of invertebrate damage and the percentage of total leaf area damaged  
284 were positively associated with July temperature and precipitation (**Table 1a**), but there was no relationship with  
285 latitude. The models estimated linear increases of the log-transformed values of herbivory with increasing July



286 temperature and precipitation (**Table 1a**), which implies smaller absolute increases in herbivory at locations with  
287 lower values of July temperature and precipitation, relative to locations with warmer and wetter summers (**Figure**  
288 **2**). For instance, the model estimates indicated a 0.4% absolute increase in the percentage of leaves damaged for  
289 every degree C increase in mean July temperature for the coldest mean July temperatures measured in our study  
290 (4.7° C). In contrast, the model estimates indicated a 1.4% absolute increase per degree C in the percentage of  
291 leaves damaged by invertebrate herbivores at locations with the highest mean July temperatures (16.7° C; **Figure**  
292 **2a**). Relative to current levels of herbivory at locations with July temperature values within the centre of the  
293 observed temperature range, these estimated values of absolute increase represent relative increases in the  
294 percentage of leaves damaged of 7.0%. Similarly, the percentage of total leaf area damaged was estimated to  
295 increase 0.04% per degree C in locations with colder summers and 0.14% per degree C in locations with warmer  
296 summers (**Figure 2b**). Relative to current levels, these figures imply predicted increases of 5.9% in leaf area  
297 damaged by invertebrate herbivores per degree C increase in mean July temperature at locations with July  
298 temperature values within the centre of the observed temperature range.

299 The potential effects of increased precipitation followed similar trends, albeit a much weaker modelled effect than  
300 temperature. With a 10 mm increase in July precipitation, the percentage of leaves damaged by invertebrate  
301 herbivores increased by 0.3% in locations with the lowest observed precipitation (10.8 mm). In contrast, at  
302 locations with the highest observed mean July precipitation measured in our study (136.3 mm), the model  
303 estimated a 0.5% absolute increase in the percentage of leaves damaged (**Figure 2c**); the increase in the  
304 percentage of leaf area damaged ranged between 0.04% and 0.11% in locations with drier and wetter summers  
305 (**Figure 2d**). Relative to current levels of invertebrate herbivory, at sites with intermediate observed levels of July  
306 precipitation, the models predicted a 3.2% relative increase in the percentage of leaves damaged and 4.3%  
307 increase in percentage of leaf area damaged per 10 mm of increased precipitation.

308 None of the covariates (birch taxa or collection date) included in the models for total herbivory were associated  
309 with the percentage of leaves damaged at each location or with the percentage leaf area damaged (**Table 1a**). The  
310 average damage per damaged leaf was not associated with latitude, temperature, precipitation, collection date or  
311 birch taxa (**Table 1a**).

### 312 *Externally feeding defoliators*

313 The percentage of leaves damaged by free-living defoliators was associated with higher July temperature and  
314 precipitation (**Table 1b**), but no latitudinal pattern was apparent. The percentage of leaf area affected by  
315 defoliators was weakly, positively related to July precipitation (**Table 1b**) but was not associated with temperature.  
316 None of the covariates explained variation in on the percentage of leaves damaged by defoliators at each location  
317 or the percentage of leaf area damaged (**Table 1b**). On average, defoliators consumed  $12.27 \pm 0.95\%$  of leaf area

318 on damaged leaves (median = 11.69%), and this value was not associated with latitude, temperature, precipitation,  
319 collection date or birch taxa (**Table 1b**).

#### 320 *Internally feeding herbivores (leaf miners and gallers)*

321 The mean percentage of leaves damaged by leaf miners at each location was  $0.55 \pm 0.17\%$  and, when present, leaf  
322 miners affected on average  $8.05 \pm 1.63\%$  of leaf area. Galls were found on  $0.08 \pm 0.05\%$  leaves per location, and  
323 affected  $35.78 \pm 8.29\%$  of the leaf area of damaged leaves. The percentage of leaves damaged by leaf miners  
324 increased with July precipitation (**Table 2a**) and the percentage of leaves damaged by gallers was associated with  
325 birch taxa, with *B. glandulosa* having a greater percentage of leaves damaged compared to *B. nana* subsp. *nana*  
326 (**Table 2**).

327

## 328 **DISCUSSION**

329 Our study is the first to provide a quantitative analysis of background invertebrate herbivory across the tundra  
330 biome. Our analysis of leaf damage on a common tundra shrub in 55 locations across the circumpolar North  
331 showed that background invertebrate herbivory is nearly ubiquitous in tundra but occurs at low intensity. On  
332 average, invertebrate herbivores consumed 1.4% of leaf area of dwarf birch and affected 11.2% of leaves. The  
333 variation in background invertebrate herbivory in tundra showed no latitudinal pattern, but both foliar losses to  
334 external feeders and the percentage of leaves damaged by internal leaf-feeders were greater at sites with higher  
335 summer temperature and precipitation.

336 General patterns of herbivory in our study were dominated by external feeding herbivores, which caused 95% of  
337 the damage. Similar to previous studies in northern areas (Kozlov 2008, Kozlov et al. 2015a) and also to the fossil  
338 record (Wilf et al. 2001), the incidence of gallers and leaf miners relative to that of defoliators was small. All  
339 studied feeding guilds of invertebrate herbivores responded positively to summer temperature and precipitation.  
340 Positive associations with temperature have been described for all three groups of herbivores in northern Europe  
341 (chewers, Kozlov et al. 2015a; leaf miners, Kozlov et al. 2013; gallers, Kozlov et al. 2016), and studies in other  
342 ecosystems have also found increased herbivory with increased precipitation for leaf chewers (Kozlov 2008,  
343 Moreira et al. 2015), leaf miners (Leckey et al. 2014) and the occurrence of galls (Leckey et al. 2014). Previous  
344 studies suggested that the contrasting responses to climate variables of different groups of herbivores would lead  
345 to different responses to changes in climate (Leckey et al. 2014, Moreira et al. 2015). Our results do not support  
346 this view for the tundra; rather, our findings suggest a generalized increase in herbivory by all feeding guilds with  
347 increased temperature and precipitation.

348 Actual summer weather in the year of data collection was found to be a better predictor of herbivory than the  
349 latitude of the study site. This is not surprising, because the relationships between climate and latitude in the  
350 Arctic are weak. For example, the position of the 10°C July isotherm varies from 50°N near Aleutian Islands to  
351 70°N in Scandinavia (CAVM Team 2003); accordingly, July temperature in our locations showed no correlation with  
352 latitude. Thus, although latitude appeared as a good predictor of invertebrate herbivory at the global scale  
353 (Pennings et al. 2009, Kozlov et al. 2015b), these trends do not hold within the tundra biome. Our study shows  
354 that biome-wide patterns of invertebrate herbivory are associated with proximal environmental cues (i.e. climatic  
355 variables) rather than latitude, and warns against the use of latitudinal gradients as analogues for climate change  
356 in the Arctic (e.g. Hodkinson and Bird 1998), unless they do really represent a climatic gradient.

357 The average damage per damaged leaf (12.1%) is comparable to previous studies (6.9%, Kozlov et al. 2015a).  
358 These relatively low levels suggest that herbivores shift their feeding sites after even low levels of damage, possibly  
359 as a result of decreases in leaf palatability in response to damage (Fisher et al. 1999, Greyson-Gaito et al. 2016).  
360 Reductions in leaf palatability may be related to the production of secondary chemical compounds in response to  
361 herbivory (Nykänen and Koricheva 2004). In northern dwarf birch the production of secondary compounds both as  
362 induced or constitutive anti-herbivore defence shows local and regional variation (Graglia et al. 2001, Torp et al.  
363 2010). For example, local topography can influence patterns of foliar concentrations of nitrogen and phenolic  
364 compounds in *B. nana* subsp. *nana* through its effects on snow accumulation and plant phenology (Torp et al.  
365 2010). This spatial variation in defensive chemistry of birch potentially accounts for the relatively constant values  
366 of damage on damaged leaves over a range of climatic conditions. However, concentrations of plant secondary  
367 metabolites appear to be poor predictors of the extent of plant damage caused by insects under natural conditions  
368 (Carmona et al. 2011) and this topic deserves further investigation, especially considering that climate change will  
369 also affect the defensive chemistry of plants (Stark et al. 2015).

370 Our models predicted that the sensitivity of invertebrate herbivory to temperature and precipitation will differ  
371 along the range of climates sampled. Given that climate models project warming of 6-10 degree C over the next  
372 100 years (IPCC 2013), the influence of temperatures on invertebrate background herbivory could be important.  
373 According to the logarithmic relationship indicated by our models, increases in invertebrate herbivory in locations  
374 with higher summer temperatures would be more pronounced than at locations with colder summers. The effect  
375 of precipitation followed similar trends but was not as pronounced and did not differ as much between the ends of  
376 the precipitation gradient. Precipitation is predicted to increase in the Arctic as a result of climate change (Cook et  
377 al. 2014), so these modest increases could, however, also be important. Differential climate sensitivities to  
378 temperatures and/or soil moisture have been also described for the phenology (Prevéy et al. 2017), community  
379 composition (Elmendorf et al. 2012) and growth (Myers-Smith et al. 2015) of tundra plants. For example, the  
380 growth of tundra shrubs was found to be more responsive to climate in wetter than in drier regions (Myers-Smith  
381 et al. 2015). Herbivory itself may also interact with climate to determine tundra plant performance. This has been

382 observed for vertebrate herbivory in tundra (Speed et al. 2011, 2013) and suggested for invertebrate herbivores  
383 (Barrio et al. 2016). In addition, climate warming has been linked to increased growth (Bret-Harte et al. 2001) and  
384 decreased investment in defense of *B. nana* subsp. *nana* (Stark et al. 2015), so while invertebrate herbivory may be  
385 expected to increase in prevalence in a warmer climate, the net outcome of climate-herbivore-plant interactions is  
386 less certain.

387 The percentage of leaves damaged on dwarf birch by invertebrate herbivores in each location varied between 0  
388 and 49% (median value was 8.7%). This has direct implications for the design of sampling protocols for detecting  
389 invertebrate damage. At least 33 leaves have to be collected to find a damaged one with a 95% probability, and 76  
390 leaves to increase this probability to 99.9%. Consequently, for damage detection on dwarf birch we would  
391 recommend that at least 100 leaves per sampling site are collected. This was the sample size that we  
392 recommended in our collection protocols and we were able to detect invertebrate herbivory in 185 out of 187  
393 sites. Larger sample sizes (~500 leaves) might be recommended to estimate leaf area losses to invertebrate  
394 herbivores with an adequate level of accuracy (Kozlov and Zvereva 2017) and to resolve the role of contrasting  
395 feeding guilds more robustly.

396 Our study supports the idea that background invertebrate herbivory could increase with current climatic changes  
397 in the tundra biome. Thus, there is an urgent need to understand how increases in the intensity of background  
398 herbivory due to rising temperatures and precipitation will affect plant performance and ecosystem functioning in  
399 tundra. Measures of leaf damage alone may not directly reflect the cost of herbivory to the plant (Lim et al. 2015),  
400 as the impact of a given amount of herbivory depends on many other factors, including the cost of production of  
401 new leaves, resource availability and plant tolerance to herbivory (Kotananen and Rosenthal 2000). The extent to  
402 which increased background invertebrate herbivory may alter tundra communities will require a comprehensive  
403 analysis of foliar damage sustained by a wide variety of species and observations over longer periods,  
404 characterization of the invertebrate herbivore fauna, and manipulative field experiments (e.g. Barrio et al. 2016).

405

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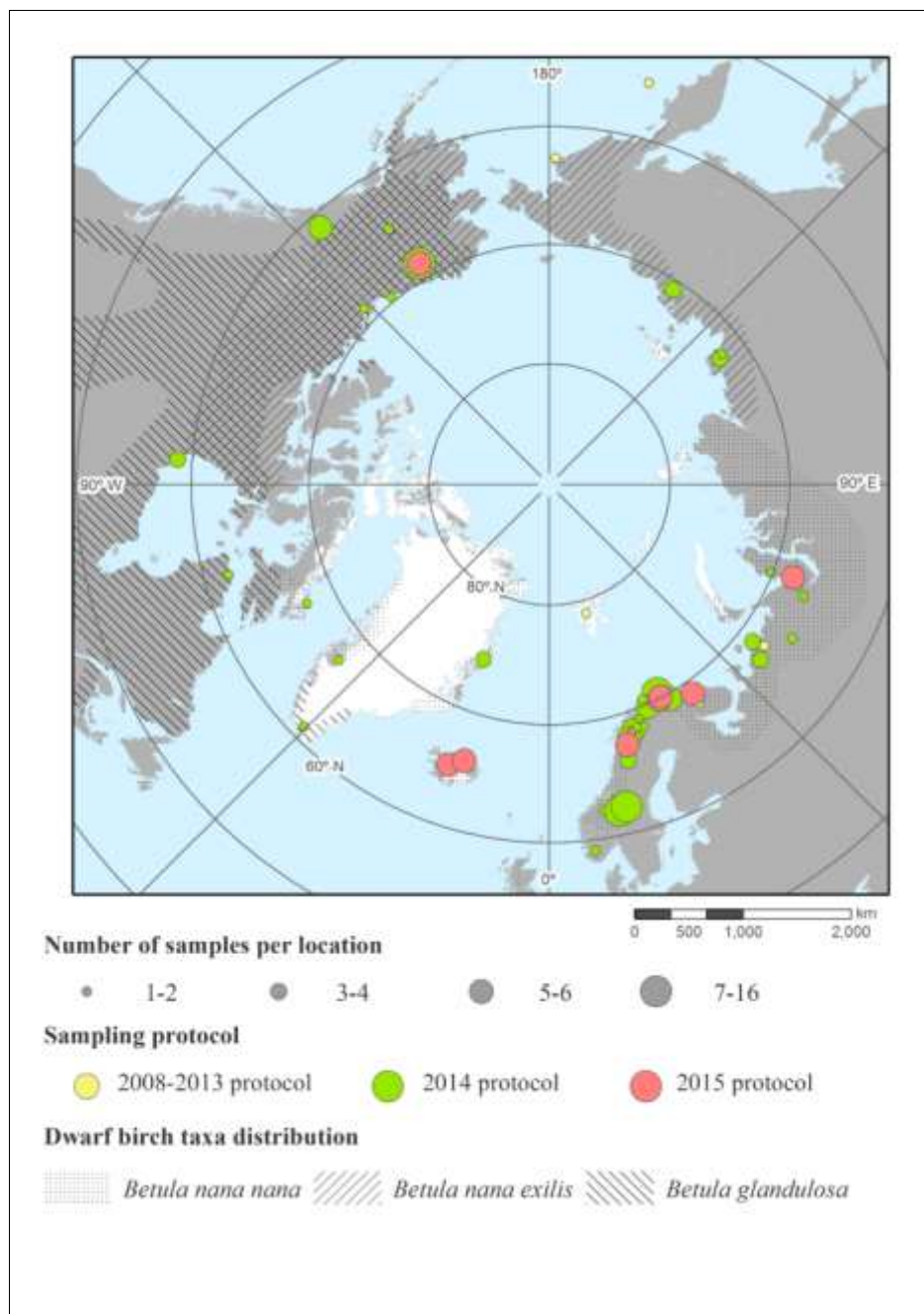
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549

550 **FIGURES**

551 **Figure 1.** Sampling locations across the tundra biome. Size of points indicates number of sites per location, and  
552 colour indicates sampling protocol used: 2008-2013 (yellow), 2014 (green) or 2015 (pink). Distribution of dwarf  
553 birch taxa is also indicated after Bryant et al (2014).

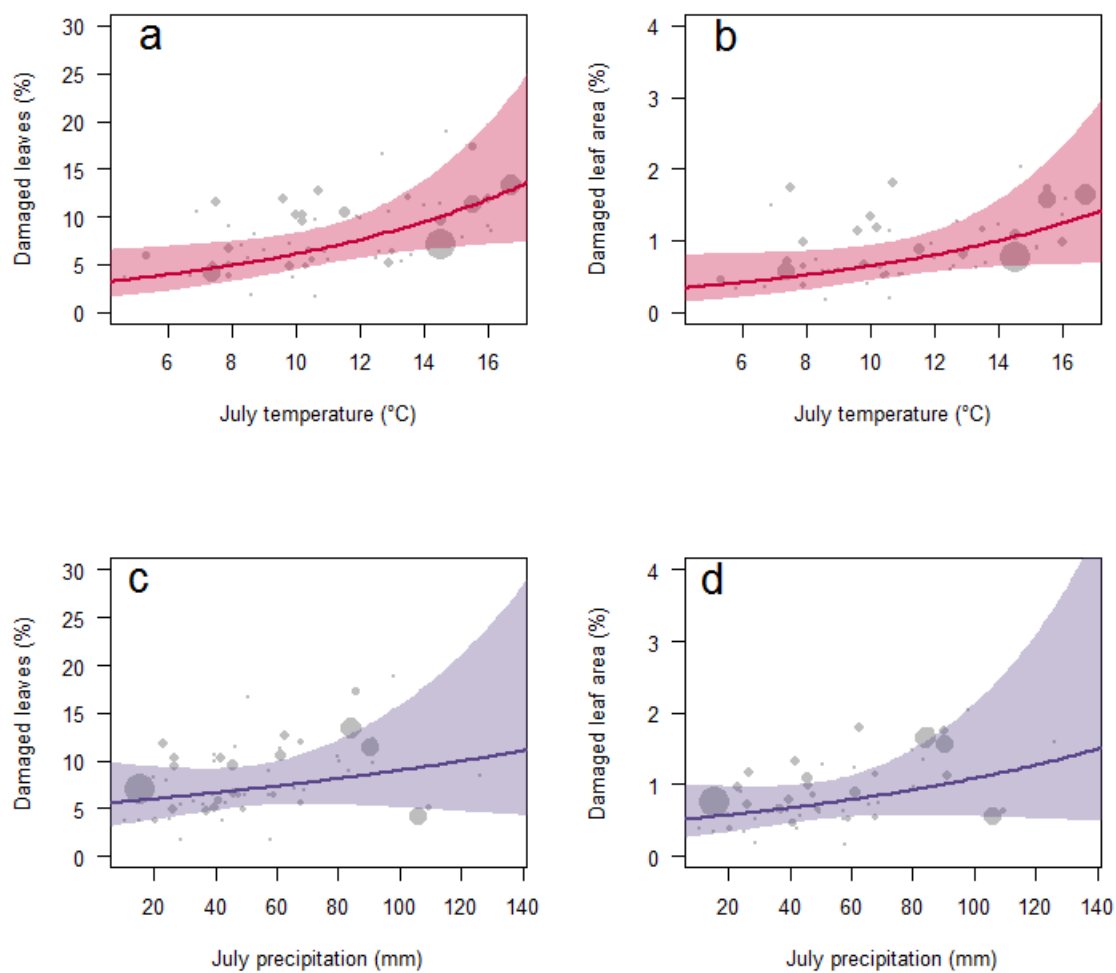


554

555



556 **Figure 2.** Relationships between the intensity of total background invertebrate herbivory and July temperatures  
557 (a,b) and precipitation (c,d): predicted values (sizes of data points are proportional to the number of samples at  
558 each location), fitted lines and confidence intervals. The intensity of herbivory was measured as the percentage of  
559 leaves damaged by invertebrates (a,c) and the percentage of leaf area affected out of all leaves examined (b,d).



560

**Table 1.** Factors explaining variation in different measures of foliar damage in dwarf birch (Linear Mixed Effect Model results) by all herbivores (a) and only defoliators (b), based on 61 samples from 55 locations across the tundra biome. Baseline for species comparisons is *Betula nana* subsp. *nana*. The percentage of leaves affected and leaf area affected were log-transformed before analyses. Estimates in bold indicate that 95% confidence interval does not include zero. Sampling protocol was included as a random effect in the models, and sample sizes at each location were included as weights. Random effects are presented as standard deviations; n indicates the number of sampling protocols, and % refer to the percentage of residual variance assigned to sampling protocol.

<b>a. All herbivores</b>						
	Percentage of leaves damaged		Percentage of leaf area damaged		Area damaged per damaged leaf	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Intercept	-2.561	-5.542, 0.421	-2.029	-5.671, 1.613	43.471	-2.223, 89.165
Latitude	0.026	-0.008, 0.061	0.017	-0.025, 0.059	-0.288	-0.816, 0.239
Temperature	<b>0.044</b>	<b>0.009, 0.080</b>	<b>0.046</b>	<b>0.003, 0.090</b>	-0.049	-0.590, 0.493
Precipitation	<b>0.005</b>	<b>0.001, 0.009</b>	<b>0.005</b>	<b>0.001, 0.010</b>	0.021	-0.041, 0.082
Species – <i>B. glandulosa</i>	0.260	-0.108, 0.628	0.138	-0.312, 0.588	2.827	-8.461, 2.807
Species – <i>B. n. exilis</i>	-0.248	-0.563, 0.067	-0.262	-0.647, 0.123	0.346	-4.483, 5.174
Collection date	0.004	-0.002, 0.010	0.000	-0.007, 0.007	0.055	-0.147, 0.037
Random effects						
Sampling protocol	0.205	(n=3, 9.5%)	0.267	(n=3, 10.6%)	2.791	(n=3, 7.6%)
Residual	0.634		0.774		9.719	
<b>b. Defoliators</b>						
	Percentage of leaves affected		Percentage of leaf area affected		Affected leaf area per damaged leaf	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Intercept	-1.586	-4.676, 1.504	-1.226	-4.944, 2.492	37.243	-10.157, 84.642
Latitude	0.021	-0.015, 0.056	0.014	-0.029, 0.057	-0.252	-0.798, 0.295
Temperature	<b>0.040</b>	<b>0.004, 0.077</b>	0.038	-0.006, 0.083	-0.187	-0.735, 0.361
Precipitation	<b>0.005</b>	<b>0.000, 0.009</b>	<b>0.005</b>	<b>0.000, 0.010</b>	0.027	-0.037, 0.090
Species – <i>B. glandulosa</i>	0.279	-0.102, 0.660	0.136	-0.323, 0.595	3.632	-9.434, 2.169
Species – <i>B. n. exilis</i>	-0.260	-0.586, 0.067	0.306	-0.699, 0.087	0.937	-5.943, 4.068
Collection date	0.002	-0.005, 0.008	0.002	-0.010, 0.005	0.031	-0.124, 0.063
Random effects						
Sampling protocol	0.206	(n=3, 8.9%)	0.267	(n=3, 10.3%)	1.778	(n=3, 3.0%)
Residual	0.659		0.790		10.105	

**Table 2.** Factors explaining variation in the percentage of leaves damaged by leaf miners (a) and gall makers (b) on dwarf birch (Linear Mixed Effect Model results), based on 61 samples from 55 locations across the tundra biome. Baseline for species comparisons is *Betula nana* subsp. *nana*. The percentage of leaves affected was log-transformed before analyses. Estimates in bold indicate that 95% confidence interval does not include zero. Sampling protocol was included as a random effect in the models, and sample sizes at each location were included as weights. Random effects are presented as standard deviations; n indicates the number of sampling protocols, and % refer to the percentage of residual variance assigned to sampling protocol.

	a. Leaf miners		b. Gall makers	
	Percentage of leaves damaged		Percentage of leaves damaged	
	Estimate	95% CI	Estimate	95% CI
Intercept	-7.261	-14.315, -0.206	-1.355	-6.101, 3.392
Latitude	0.032	-0.049, 0.113	-0.005	-0.050, 0.059
Temperature	0.070	-0.014, 0.154	0.012	-0.041, 0.066
Precipitation	<b>0.010</b>	<b>0.001, 0.020</b>	0.005	-0.001, 0.012
Species – <i>B. glandulosa</i>	0.182	-1.054, 0.689	<b>0.687</b>	<b>0.111, 1.264</b>
Species – <i>B. n. exilis</i>	0.142	-0.887, 0.603	0.360	-0.141, 0.860
Collection date	0.013	-0.002, 0.027	-0.006	-0.015, 0.004
Random effects				
Sampling protocol	0.582	(n=3, 13.1%)	0.118	(n=3, 1.3%)
Residual	1.497		1.013	