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ABSTRACT

78   Chronic, low intensity herbivory by invertebrates, termed background herbivory, has been understudied in tundra,

79   yet its impacts are likely to increase in a warmer Arctic. The magnitude of these changes is however hard to

80   predict as we know little about the drivers of current levels of invertebrate herbivory in tundra. We assessed the

81   intensity of invertebrate herbivory on a common tundra plant, the dwarf birch (*Betula glandulosa-nana* complex),

82   and investigated its relationship to latitude and climate across the tundra biome. Leaf damage by defoliating,

83   mining and gall-forming invertebrates was measured in samples collected from 192 sites at 56 locations. Our

84   results indicate that invertebrate herbivory is nearly ubiquitous across the tundra biome but occurs at low

85   intensity. On average, invertebrates damaged 11.2% of the leaves and removed 1.4% of total leaf area. The

86   damage was mainly caused by external leaf feeders, and most damaged leaves were only slightly affected (12%

87   leaf area lost). Foliar damage was consistently positively correlated with mid-summer (July) temperature and, to a

88   lesser extent, precipitation in the year of data collection, irrespective of latitude. Our models predict that, on

89   average, foliar losses to invertebrates on dwarf birch are likely to increase by 6-7% over the current levels with a 1

90   °C increase in summer temperatures. Our results show that invertebrate herbivory on dwarf birch is small in

91   magnitude but given its prevalence and dependence on climatic variables, background invertebrate herbivory

92   should be included in predictions of climate change impacts on tundra ecosystems.

93   **Keywords:** background insect herbivory, climate change, externally feeding defoliators, Latitudinal Herbivory

94   Hypothesis, leaf damage, leaf miners, gall-makers, macroecological pattern

INTRODUCTION

95

96 The role of invertebrate herbivores in tundra ecosystems has been understudied (Haukioja 1981). Admittedly, the

97 proportion of herbivore taxa among invertebrates is lower in Arctic regions than at lower latitudes (Danks 1986),

98 and invertebrate herbivores generally occur at relatively low abundances in tundra (Haukioja 1981). However,

99 outbreaks of invertebrate herbivores have been well documented in the forest-tundra ecotone (Jepsen et al. 2008;

100 Kaukonen et al. 2013) and occasionally in tundra (Post and Pedersen 2008). These massive defoliation events have

101 large impacts on subarctic birch forests, enhancing resource turnover through deposition of frass and carcasses to

102 the soil (Kaukonen et al. 2013) and causing vegetation shifts from forested to open conditions with consequences

103 for ecosystem functioning and trophic interactions (Jepsen et al. 2013; Olofsson et al. 2013; Parker et al. 2016). In

104 contrast, chronic leaf consumption by invertebrate herbivores when they occur at low densities, termed

105 background herbivory (Kozlov and Zvereva 2017), has long been assumed to be unimportant, especially in the

106 Arctic (Batzli et al. 1980; Haukioja 1981). However, recent studies in boreal forest indicate that chronic

107 invertebrate herbivory can have stronger impacts on plant growth in the long term than infrequent bouts of severe

108 damage (Zvereva et al. 2012), and can play a major role in ecosystem-level nutrient cycling (Metcalfe et al. 2016).

109 Yet, the extent, drivers and consequences of background herbivory across the tundra biome remain unquantified

110 (Kozlov et al. 2015b).

111 The Latitudinal Herbivory Hypothesis (LHH) suggests that the intensity of herbivory should decrease with

112 increasing latitude (Coley and Aide 1991; Johnson and Rasmann 2011). In its original formulation, it was argued

113 that a wider diversity of specialist herbivores in tropical areas, together with warmer temperatures and a longer

114 growing season, could lead to increased herbivory rates at lower latitudes. Empirical evidence has found support

115 for LHH at the global scale, demonstrating that invertebrate herbivory of woody plants is generally lower in the

116 polar regions than in temperate and tropical zones (Kozlov et al. 2015a). However, the generality of the LHH

117 across plant functional types, invertebrate species and spatial scales is still debated (Moles et al. 2011; Anstett et

118 al. 2016; Zhang et al. 2016). Latitudinal patterns with increased levels of herbivory at lower latitudes have been

119 described for some species of plants and groups of insect herbivores (Kozlov 2008; Pennings et al. 2009; Moreira et

120 al. 2015; Kozlov et al. 2016), but lack of latitudinal trends (Andrew and Hughes 2005; Kozlov 2008; Pennings et al.

121 2009), higher levels of herbivory at higher latitudes (Moreira et al. 2015; Kozlov et al. 2016), or even dome-shaped

122 patterns (Kozlov et al. 2015a) have been described for others. Moreover, such studies have typically been

123 conducted in temperate regions; whether latitudinal patterns can be found within the tundra biome remains

124 unknown. Similarly, the mechanisms behind these macroecological patterns in background herbivory are poorly

125 understood. Biotic and abiotic factors vary with latitude and this variability may promote variation in herbivory.

126 For example, it has been suggested that, along with direct effects of climate, latitudinal gradients in herbivory may

127 be shaped by changes in plant defensive chemistry (Moles et al. 2011), in predator pressure (Björkman et al. 2011)

128 or by variations in leaf toughness (Onoda et al. 2011).

4

129   Climatic variables are usually considered one of the main drivers of latitudinal patterns in the intensity of biotic

130   interactions. Temperature directly affects the performance and abundance of invertebrate herbivores (Bale et al.

131   2002), since their physiology, population growth and dynamics are generally controlled by temperature

132   (Hodkinson and Bird 1998). Temperature could also affect invertebrate herbivores indirectly, through changes in

133   the palatability or availability of their host plants (Bale et al. 2002). Warmer temperatures have been associated

134   with increased levels of herbivory in the fossil record (Wilf and Labandeira 1999; Wilf et al. 2001) and in

135   experimental field studies (Richardson et al. 2002; Roy et al. 2004). Temperature was also found to explain

136   latitudinal patterns in background herbivory in northern boreal forests (Kozlov 2008), as well as annual variations

137   in this pattern (Kozlov et al. 2013), with higher temperatures associated with increased levels of herbivory. The

138   effects of precipitation on the levels and types of invertebrate herbivory have been studied less systematically

139   (Bale et al. 2002). Temperature was found to be a better predictor of herbivory than precipitation at a global scale

140   (Kozlov et al. 2015a; Zhang et al. 2016), yet precipitation has a stronger influence on the global patterns of leaf

141   traits related to resistance to damage, with more resistant leaves in sites with lower annual precipitation (Onoda

142   et al. 2011). Broad gradients of temperature and precipitation exist across the tundra biome; we therefore

143   hypothesize that patterns of invertebrate herbivory will also be influenced by climatic gradients in this region.

144   Patterns of herbivory and their underlying mechanisms may also differ between feeding guilds of herbivores with

145   contrasting life history traits (Hiura and Nakamura 2013; Anstett et al. 2014). Some studies have found that

146   geographical patterns in the abundance of different herbivores or the intensity of herbivory were driven by

147   different climatic variables, suggesting that variation in the sensitivity of feeding guilds to climate could lead to

148   disparate predictions under climate change (Leckey et al. 2014; Moreira et al. 2015). For example, externally

149   feeding defoliators are more exposed to abiotic variables and may respond to them directly, whereas internally

150   feeding herbivores like leaf miners and gallers may be affected by abiotic variables indirectly through their effects

151   on leaf traits (e.g. Andrew and Hughes 2005, Sinclair and Hughes 2008). For instance, precipitation affects the

152   intensity of herbivory by leaf miners and gall-makers (Leckey et al. 2014), possibly through its effects on leaf

153   toughness (Onoda et al. 2011). Tougher leaves are well defended against external herbivores but may favour

154   internally feeding herbivores as they provide safer shelter against pathogens and reduce levels of desiccation

155   (Carneiro et al. 2005). We propose that the same distinction between external and internal feeders will drive

156   differences in the patterns of invertebrate herbivory in tundra.

157   Temperatures and precipitation are predicted to continue increasing in the Arctic (Cook et al. 2014), and warming

158   in tundra is expected to occur at a higher rate than the global average (IPCC 2013). The rapid pace of

159   environmental changes in the Arctic underscores the urgency of studying the responses of fundamental ecological

160   processes, such as herbivory, to varying climatic conditions. Insects living at higher latitudes are highly responsive

161   to climate changes (Hodkinson and Bird 1998), and warming-induced increases in insect herbivory are expected to

162   be stronger at higher latitudes (Wolf et al. 2008; Kozlov et al. 2015a). Experimental studies in tundra have shown

163   that the intensity of invertebrate herbivory increases with warming (Barrio et al. 2016; Birkemoe et al. 2016), but

164   the lack of knowledge on current levels of background herbivory across the tundra biome constrains any

165   meaningful predictions.

166   The objective of this study is to assess the intensity of background invertebrate herbivory and characterise its

167   relationships with latitude and climatic variables in tundra. To achieve this goal, we measured leaf damage by

168   tissue-feeding invertebrate herbivores on a common tundra plant with a circumpolar distribution, the dwarf birch

169   (*Betula glandulosa-nana* complex), across a large number of sites spanning nearly 24° of latitude. Dwarf birch is a

170   main food plant of many tundra herbivores (Koponen 1984; Bryant et al. 2014) and it is an important component in

171   shrub tundra plant communities. The wide distribution of dwarf birch facilitates comparisons within a single host

172   plant across a latitudinal gradient (Anstett et al. 2016); further, the range and abundance of dwarf birch are

173   predicted to expand in response to warming (Euskirchen et al. 2009; Myers-Smith et al. 2011). We test the

174   following hypotheses: (i) background invertebrate herbivory within the tundra biome is greatest at lower latitudes,

175   consistent with the LHH, or where summer temperature and precipitation are highest; and (ii) the patterns of

176   invertebrate herbivory by different feeding guilds will correspond with different climatic variables, given their

177   sensitivity to different environmental cues. Specifically, we expect leaf damage by externally-feeding defoliators to

178   be more strongly associated with summer temperature than damage by internally feeding herbivores (leaf miners

179   and gallers), and conversely that the latter will be more affected by climatic variables that determine leaf

180   toughness, such as precipitation.

181

182   **METHODS**

183   *Focal plant species and leaf sampling*

184   Dwarf birch is a taxonomic complex with several closely related and hybridizing species. The main taxonomic units

185   that we identified are *Betula glandulosa* Michx., *B. nana* subsp. *nana* L. and *B. nana* subsp. *exilis* (Sukaczev) Hultén.

186   Species identification was conducted by collectors in the field and verified based on distribution maps (**Figure 1**;

187   Bryant et al. 2014). *Betula glandulosa* is distributed throughout the northern regions of North America, from

188   Alaska to Newfoundland, as well as the southern part of Greenland (Feilberg 1984). *Betula nana* is distributed

189   throughout the Arctic regions of Eurasia and North America, with *B. nana* subsp. *nana* occurring from Greenland

190   through northern Europe to Western Siberia, and *B. nana* subsp. *exilis* occurring from Eastern Siberia to Alaska and

191   into northern Canada (Bryant et al. 2014). These three taxonomic units differ in leaf chemistry: *B. nana* subsp.

192   *exilis* and *B. glandulosa* have higher concentrations of phenolic glycosides, condensed tannins, and triterpenes,

193   have lower leaf nitrogen, and are less palatable to vertebrate herbivores than *B. nana* subsp. *nana* (Bryant et al.

194   2014; DeAngelis et al. 2015). However, the importance of these chemical differences for invertebrate herbivory is

195   not known.

196   Plant material was collected in the summers of 2008-2013 (summarized by Kozlov et al. 2015b), 2014 and 2015

197   between June 12 and September 17. Although different protocols were followed in different years (**Table 1**),

198   samples were collected in a way that allowed for spatial comparisons to evaluate background herbivory and its

199   relationship to abiotic conditions. The protocol used in 2008-2013 (see Appendix S2 to Kozlov et al. 2015b) aimed

200   at sampling plant foliage for measurements of insect herbivory at the global scale. The 2014 protocol was

201   designed to assess defensive chemistry of dwarf birches across the Arctic (**Online Resource S1**); for the purpose of

202   this study we only used one of the two top shoot samples collected in 2014 (both long and short shoots). We

203   disregarded the samples specifically collected from short shoots (primary growth), as they may not be

204   representative of herbivory on the whole plant. The 2015 protocol was aimed at measuring background

205   invertebrate herbivory in tundra at the plant community level

206   (http://herbivory.biology.ualberta.ca/files/2016/11/background_herbivory_tundra.pdf); here we report only the

207   results for dwarf birch.

208   Briefly, all sampling protocols requested collection of birch leaves from several individuals per site (2-5 individuals

209   were sampled in 2008-2013, 10 individuals in 2014, and 3 individuals in 2015). The samples included 71-500 leaves

210   per site, where sites were defined as circular areas of approximately 10 m radius, at least 100 m apart. The

211   number of sites within a location (i.e. spatially distinct 'study areas', at least 10 km apart) varied between 1 and 16

212   (for the 2008-2013 and 2014 protocols, a minimum of 1 site per location was requested, while for the 2015

213   protocol, the minimum number of sites per location was 5). Samples were collected from 192 sites in 56 locations

214   (**Table 1**), spanning 23.7° of latitude across the tundra biome (including non-Arctic locations in alpine areas), from

215   55.2° N to 78.9° N (**Figure 1; Online Resource S2**). The geographical distribution of locations was not designed in

216   advance: the requests for sampling were distributed across the research community, and all samples received

217   were included in our study.

218   *Leaf damage assessment*

219   Each leaf was inspected on both sides for leaf damage with a light source against the leaf to detect damage on the

220   surface, and then with the light through the leaf, to detect damage inside the leaf. We distinguished damage

221   caused by three different feeding guilds of invertebrate herbivores: external leaf feeders (chewing or

222   skeletonization) and internally feeding miners and gall makers (**Online Resource S3**). External feeding damage on

223   dwarf birch is caused primarily by sawflies (Hymenoptera: Tenthredinidae) and by moth larvae (Lepidoptera)

224   (Koponen 1984). Leaf miners can include larvae of Lepidoptera and Coleoptera (Viramo 1962), whereas galls are

225   formed by insects and eriophyid mites. Other herbivores, such as phloem-feeders, also occur on dwarf birch

226   (Koponen 1984), but damage imposed by these insects could not be measured from leaf samples.

227 Following a widely used methodology (Kozlov and Zvereva 2017, and references therein), each leaf was assigned to
228 a damage class according to the each type of damage (multiple damage types on the same leaf occurred in less
229 than 1% of leaves analysed) and to the visually estimated percentage of the leaf area damaged by invertebrates:
230 intact leaves, 0.01-1, 1-5, 5-25, 25-50, 50-75 and 75-100% (Kozlov 2008). Samples from the three protocols were
231 evaluated by three scorers (2008-2013 protocol by MVK, 2014 by EL, 2015 by ICB); assessments made by the three
232 scorers on 6-10 training samples (100 leaves each) indicated no statistically significant effect of the scorer on the
233 estimates of foliar damage (pairwise t-test: all $p>0.1$; intra-class correlation coefficients ranged between 0.56 and
234 0.88).

235 *Data analysis*

236 The intensity of invertebrate herbivory at each site was calculated using three complementary measures: 1)
237 percentage of leaves damaged: the percentage of leaves that showed signs of invertebrate herbivory at a site; 2)
238 percentage of leaf area damaged: the percentage of leaf area consumed or otherwise damaged by invertebrate
239 herbivores over the total number of leaves inspected in a sample; and 3) average damage per damaged leaf: the
240 average leaf area consumed or otherwise damaged by invertebrate herbivores per damaged leaf. The percentage
241 of leaves damaged indicates the distribution of damage within a site; the percentage of leaf area damaged gives an
242 approximation of foliar loss per site as a measure of herbivory; and the average damage per damaged leaf reflects
243 how much of the leaf area is affected, once a leaf is damaged (Kozlov 2008; Kozlov et al. 2015b). To calculate the
244 latter two variables, the number of leaves in each damage class was multiplied by the corresponding median value
245 of damage (i.e. 0 for intact leaves, 0.5% for the 0.01-1% class, 3% for the 1-5% class, 15% for the 5-25% class,
246 37.5% for the 25-50% class, 62.5% for the 50-75% class, and 87.5% for the 75-100% class) and summed for all
247 damage classes. These values were divided by the total number of leaves to obtain an estimate of the percentage
248 of total leaf area damaged, and by the number of damaged leaves to obtain the average damage per damaged leaf
249 (Kozlov et al. 2015a; Kozlov et al. 2015b). All variables were calculated for all invertebrate herbivores and for the
250 three different feeding guilds separately (**Online Resource S2**); given the low occurrence of mines and galls, only
251 the percentage of leaves damaged was included in the models for these groups.

252 To investigate the effects of latitude and climatic variables on invertebrate herbivory in tundra we built Linear
253 Mixed Effects Models for total herbivory and for each feeding group separately. In all models, sampling protocol
254 (2008-2013, 2014 or 2015) was included as a random effect to account for potential confounding effects of year of
255 sampling, person scoring leaf damage and/or protocol design. Nearly half of the sampling locations (25 out of 62)
256 sampled one site only, so location could not be included in the models as a random factor; therefore,
257 measurements of invertebrate herbivory for locations with more than one site were averaged across sites, and the
258 number of sites sampled at each location was included as weights in the models to account for differences in
259 sampling effort.

260   We extracted the following indices as potential predictors of background herbivory: mean July temperature in the

261   year of sampling, annual temperature, temperature seasonality (standard deviation of annual temperature),

262   maximum temperature of the warmest month, minimum temperature of the coldest month, mean temp of

263   warmest quarter (Jun-Aug), total July precipitation in the year of sampling, annual precipitation and precipitation

264   seasonality (coefficient of variation). Initial correlation analyses indicated that mean July temperature and total

265   July precipitation in the year of sampling had the highest correlations with measures of herbivory (**Online Resource**

266   **S4**), so these two climate variables and latitude were included as predictors in the models. These two climate

267   variables were extracted from the Global Historical Climatology Network-Monthly (GHCN-M v3.2.1, Lawrimore et

268   al. 2011). This dataset provides monthly mean temperatures and precipitation as a spatial raster (0.5 degree

269   resolution) based on weather station data. We extracted July temperature and precipitation for the year of

270   sample collection, because current-season weather is more relevant to invertebrate herbivory than multi-year

271   averages (Kozlov et al. 2013). Climate variables and latitude were included as predictors in the models.

272   Correlations between continuous predictor variables were low (r<0.4; **Online Resource S4**) and Variance Inflation

273   Factors indicated no strong multicollinearity (VIF<1.2), so all three variables were included simultaneously in the

274   models. Dwarf birch exhibits patterns of regional and taxonomic variation in defense against browsing by

275   vertebrates (Bryant et al. 2014) that may also affect the observed patterns of invertebrate herbivory, so we

276   included dwarf birch taxon (*B. glandulosa, B. nana* subsp. *exilis* and *B.nana* subsp. *nana*) as a fixed effect variable

277   in our analyses. We also included collection date, measured as day-of-year, as a fixed covariate in the models

278   because foliar damage accumulates over the growing season, but damaged leaves tend to abscise prematurely

279   (Torp et al. 2010; Kozlov et al. 2016). For the two locations where no invertebrate leaf damage was detected

280   (Svalbard and Beringa Island), we assigned the lowest possible value for herbivory (0.1% for the percentage of

281   leaves damaged by all herbivores and defoliators, 0.01% in the case of leaf miners and gallers, and 0.01% for leaf

282   area damaged). The percentage of damaged leaves and the percentage leaf area affected by herbivory were then

283   log-transformed to comply with model assumptions of normality and homogeneity of variances, which were

284   checked by visually inspecting model residuals (Zuur et al. 2009). All analyses were run in R 3.2.3 (R Development

285   Core Team 2015) using the *lme4* package to build Linear Mixed Effects Models (Bates et al. 2015).

286

287   **RESULTS**

288   Feeding marks of invertebrate herbivores were found on 3,949 of the 30,817 leaves examined (12.8%). Damage by

289   invertebrate herbivores affected between 0 and 46.0% of leaves at each location (mean ± SE: 11.2 ± 1.3%; median=

290   8.8%, n=62; **Online Resource S5**). On average, 1.4 ± 0.2% of leaf area was damaged at each location (median =

291   1.1%), and most damaged leaves were only slightly affected (12.0 ± 0.9% of leaf area damaged; median = 11.8%).

292   The vast majority of damage (98.6%) was caused by defoliators. Damage by internally feeding herbivores (leaf

293   miners and gallers) was found on relatively few leaves: 31 were mined by larvae of several moth species and only

294   24 bore galls (see **Online Resource S6** for identification of mines and galls).

295   *Total herbivory*

296   Both the percentage of leaves with signs of invertebrate damage and the percentage of total leaf area damaged

297   were positively associated with July temperature and precipitation (**Table 2a**), but there was no relationship with

298   latitude. The models estimated linear increases of the log-transformed values of herbivory with increasing July

299   temperature and precipitation (**Table 2a**), which implies smaller absolute increases in herbivory at locations with

300   lower values of July temperature and precipitation, relative to locations with warmer and wetter summers (**Figure**

301   **2**). For instance, the model estimates indicated a 0.4% absolute increase in the percentage of leaves damaged for

302   every degree C increase in mean July temperature for the coldest mean July temperatures measured in our study

303   (4.7° C; **Figure 2a**). In contrast, the model estimates indicated a 1.7% absolute increase per degree C in the

304   percentage of leaves damaged by invertebrate herbivores at locations with the highest mean July temperatures

305   (16.7° C; **Figure 2a**). Relative to current levels of herbivory (11.2% leaves damaged), these estimated values of

306   absolute increase at locations with July temperature values within the centre of the observed temperature range

307   (absolute increase 0.93%), represent relative increases in the percentage of leaves damaged of 8.3%. Similarly, the

308   percentage of total leaf area damaged was estimated to increase 0.04% per degree C in locations with colder

309   summers and 0.17% per degree C in locations with warmer summers (**Figure 2b**). Relative to observed current

310   levels of leaf area damaged (1.4%), these figures imply predicted increases of 6.7% in leaf area damaged by

311   invertebrate herbivores per degree C increase in mean July temperature, at locations with July temperature values

312   within the centre of the observed temperature range (mean July temperature observed across sites = 11.4° C).

313   The potential effects of increased precipitation followed similar trends, albeit a much weaker modelled effect than

314   temperature. With a 10 mm increase in July precipitation, the percentage of leaves damaged by invertebrate

315   herbivores increased by 0.3% in locations with the lowest observed precipitation (10.8 mm). In contrast, at

316   locations with the highest observed mean July precipitation measured in our study (136.3 mm), the model

317   estimated a 0.6% absolute increase in the percentage of leaves damaged (**Figure 2c**); the increase in the

318   percentage of leaf area damaged ranged between 0.05% and 0.12% in locations with drier and wetter summers

319   (**Figure 2d**). Relative to current levels of invertebrate herbivory, at sites with intermediate observed levels of July

320   precipitation (mean total July precipitation observed across sites = 53.2 mm), the models predicted a 3.6% relative

321   increase in the percentage of leaves damaged and 4.5% increase in percentage of leaf area damaged per 10 mm of

322   increased precipitation.

323   None of the covariates (birch taxa or collection date) included in the models for total herbivory were associated

324   with the percentage of leaves damaged at each location or with the percentage leaf area damaged (**Table 2a**). The

325 average damage per damaged leaf was not associated with latitude, temperature, precipitation, collection date or

326 birch taxa (**Table 2a**).

327 *Externally feeding defoliators*

328 The distribution of damage by free-living defoliators within a site, as measured with the percentage of leaves

329 damaged was associated with higher July temperature and precipitation (**Table 2b**), but no latitudinal pattern was

330 apparent. When looking at foliar loss, the percentage of leaf area affected by defoliators was positively, albeit

331 weakly, related to July precipitation and temperature (**Table 2b**). None of the covariates explained variation in on

332 the percentage of leaves damaged by defoliators at each location or the percentage of leaf area damaged (**Table**

333 **2b**). On average, defoliators consumed 11.09 ± 1.26% of leaf area on damaged leaves (median = 8.56%), and this

334 value was not associated with latitude, temperature, precipitation, collection date or birch taxa (**Table 2b**).

335 *Internally feeding herbivores (leaf miners and gallers)*

336 The mean percentage of leaves damaged by leaf miners at each location was 0.06 ± 0.02% and, when present, leaf

337 miners affected on average 11.77 ± 3.05% of leaf area. Galls were found on 0.08 ± 0.05% leaves per location, and

338 affected 35.78 ± 8.29% of the leaf area of damaged leaves (excluding 2 galled leaves with petiole galls). The

339 percentage of leaves damaged by leaf miners increased with July precipitation and collection date (**Table 3a**) and

340 the percentage of leaves damaged by gallers was associated with birch taxa, with *B. glandulosa* having a greater

341 percentage of leaves damaged compared to *B. nana* subsp. *nana* (**Table 3b**).

342

343 **DISCUSSION**

344 Our study is the first to provide a quantitative analysis of background invertebrate herbivory across the tundra

345 biome. Our analysis of leaf damage on a common tundra shrub in 56 locations across the circumpolar North

346 showed that background invertebrate herbivory is nearly ubiquitous in tundra but occurs at low intensity. On

347 average, invertebrate herbivores consumed 1.4% of leaf area of dwarf birch and affected 11.2% of leaves. The

348 variation in background invertebrate herbivory in tundra showed no latitudinal pattern, but both foliar losses to

349 external feeders and the percentage of leaves damaged by internal leaf-feeders were greater at sites with higher

350 summer temperature and precipitation. Contrary to our expectations, all feeding guilds responded to the different

351 climatic variables in a similar way.

352 General patterns of herbivory in our study were dominated by external feeding herbivores, which caused over 98%

353 of the damage. Similar to previous studies in northern areas (Kozlov 2008; Kozlov et al. 2015b) and also in the fossil

354 record (Wilf et al. 2001), the incidence of gallers and leaf miners relative to that of defoliators was very small.

355 Although previous studies suggested that different groups of herbivores may respond differently to climate

356 variables (Leckey et al. 2014; Moreira et al. 2015), our results do not support this view for the tundra; rather, our

357 findings suggest a generalized increase in herbivory by all feeding guilds with increased temperature and

358 precipitation. Such positive associations with temperature have already been described for these three groups of

359 herbivores in northern Europe (chewers, Kozlov et al. 2015a; leaf miners, Kozlov et al. 2013; gallers, Kozlov et al.

360 2016). Similarly, studies in other ecosystems have also found increased herbivory with increased precipitation for

361 leaf chewers (Kozlov 2008; Moreira et al. 2015), leaf miners (Leckey et al. 2014) and the occurrence of galls (Leckey

362 et al. 2014).

363 Actual summer weather in the year of data collection was found to be a better predictor of herbivory than the

364 latitude of the study site. This is not surprising, because the relationships between climate and latitude in the

365 Arctic are weak. For example, the position of the 10°C July isotherm varies from 50°N near Aleutian Islands to

366 70°N in Scandinavia (CAVM Team 2003); accordingly, July temperature in our locations showed no correlation with

367 latitude. Thus, although latitude appeared as a good predictor of invertebrate herbivory at the global scale

368 according to the LHH (Pennings et al. 2009; Kozlov et al. 2015a), these trends do not hold within the tundra biome.

369 Our study shows that biome-wide patterns of invertebrate herbivory are associated with proximal environmental

370 cues (i.e. climatic variables) rather than with latitude, and warns against the use of latitudinal gradients as

371 analogues for climate change in the Arctic (e.g. Hodkinson and Bird 1998), unless they do really represent a

372 climatic gradient.

373 The average damage per damaged leaf (12.1%) is comparable to previous studies (6.9%, Kozlov et al. 2015a).

374 These relatively low levels suggest that herbivores shift their feeding sites after even low levels of damage, possibly

375 as a result of decreases in leaf palatability in response to damage or as a strategy to avoid detection by natural

376 enemies (Fisher et al. 1999; Greyson-Gaito et al. 2016). Reductions in leaf palatability may be related to the

377 production of secondary chemical compounds in response to herbivory (Nykänen and Koricheva 2004). In

378 northern dwarf birch the production of secondary compounds both as induced or constitutive anti-herbivore

379 defence shows local and regional variation (Graglia et al. 2001; Torp et al. 2010). For example, local topography

380 can influence patterns of foliar concentrations of nitrogen and phenolic compounds in *B. nana* subsp. *nana*

381 through its effects on snow accumulation and plant phenology (Torp et al. 2010). This spatial variation in

382 defensive chemistry of birch potentially accounts for the relatively constant values of damage on damaged leaves

383 over a range of climatic conditions. However, concentrations of plant secondary metabolites appear to be poor

384 predictors of the extent of plant damage caused by insects under natural conditions (Carmona et al. 2011). The

385 use of broad metrics, such as total phenolics, to measure resistance against herbivores or comparisons across

386 unrelated species may obscure the importance of secondary compounds (Agrawal and Weber 2015; Anstett et al.

387 2015). This topic deserves further investigation, especially considering that climate change will also affect the

388 defensive chemistry of plants. For example, phenolic compounds are expected to decrease with increased

389 temperature (Stark et al. 2015), but the response to warming might differ depending on what type and

390 combination of secondary metabolites plants have (Graglia et al. 2001).

391 Our models predicted that changes in invertebrate herbivory in response to temperature and precipitation will

392 differ along the range of climates sampled. It must be kept in mind that our approach represents a space-for-time

393 substitution, where we infer changes in herbivory from locations with different climatic variables. Despite its

394 limitations, this approach provides the best solution given the virtual lack of long-term trend data in patterns of

395 invertebrate herbivory in tundra over time. Given that climate models project warming of 6-10 degree C over the

396 next 100 years (IPCC 2013), the influence of temperatures on invertebrate background herbivory could be

397 important. According to the logarithmic relationship indicated by our models, increases in invertebrate herbivory

398 in locations with higher summer temperatures would be more pronounced than at locations with colder summers.

399 The effect of precipitation followed similar trends but was not as pronounced and did not differ as much between

400 the ends of the precipitation gradient. Precipitation is predicted to increase in the Arctic as a result of climate

401 change (Cook et al. 2014), so these modest increases could, however, also be important. Differential climate

402 sensitivities to temperatures and/or soil moisture have been also described for the phenology (Prevéy et al. 2017),

403 community composition (Elmendorf et al. 2012) and growth (Myers-Smith et al. 2015) of tundra plants. For

404 example, the growth of tundra shrubs was found to be more responsive to climate in wetter than in drier regions

405 (Myers-Smith et al. 2015). Herbivory itself may also interact with climate to determine tundra plant performance.

406 This has been observed for vertebrate herbivory in tundra (Speed et al. 2011; Speed et al. 2013) and suggested for

407 invertebrate herbivores (Barrio et al. 2016). In addition, climate warming has been linked to increased growth

408 (Bret-Harte et al. 2001) and decreased investment in defense of *B. nana* subsp. *nana* (Stark et al. 2015), so while

409 invertebrate herbivory may be expected to increase in prevalence in a warmer climate, the net outcome of

410 climate-herbivore-plant interactions is less certain.

411 The percentage of leaves damaged on dwarf birch by invertebrate herbivores in each location varied between 0

412 and 49% (median value was 8.7%). This has direct implications for the design of sampling protocols for detecting

413 invertebrate damage. At least 33 leaves have to be collected to find a damaged one with a 95% probability, and 76

414 leaves to increase this probability to 99.9%. Consequently, for damage detection on dwarf birch we would

415 recommend that at least 100 leaves per sampling site are collected. This was the sample size that we

416 recommended in our collection protocols and we were able to detect invertebrate herbivory in 185 out of 187

417 sites. Larger sample sizes (~500 leaves) might be recommended to estimate leaf area losses to invertebrate

418 herbivores with an adequate level of accuracy (Kozlov and Zvereva 2017) and to resolve the role of contrasting

419 feeding guilds more robustly.

420 Our study supports the idea that background invertebrate herbivory could increase with current climatic changes

421 in the tundra biome. Thus, there is an urgent need to understand how increases in the intensity of background

422 herbivory due to rising temperatures and precipitation will affect plant performance and ecosystem functioning in

423 tundra. Measures of leaf damage alone may not directly reflect the cost of herbivory to the plant (Lim et al. 2015),

424 as the impact of a given amount of herbivory depends on many other factors, including the cost of production of

425 new leaves, resource availability and plant tolerance to herbivory (Kotanen and Rosenthal 2000). The extent to

426 which increased background invertebrate herbivory may alter tundra communities will require a comprehensive

427 analysis of foliar damage sustained by a wide variety of species and observations over longer periods,

428 characterization of the invertebrate herbivore fauna, and manipulative field experiments (e.g. Barrio et al. 2016).

429

450

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585

FIGURES

Figure 1. Sampling locations across the tundra biome. Size of points indicates number of sites per location, and colour indicates sampling protocol used: 2008-2013 (black), 2014 (grey) or 2015 (white). Distribution of dwarf birch taxa is indicated after Bryant et al. (2014).
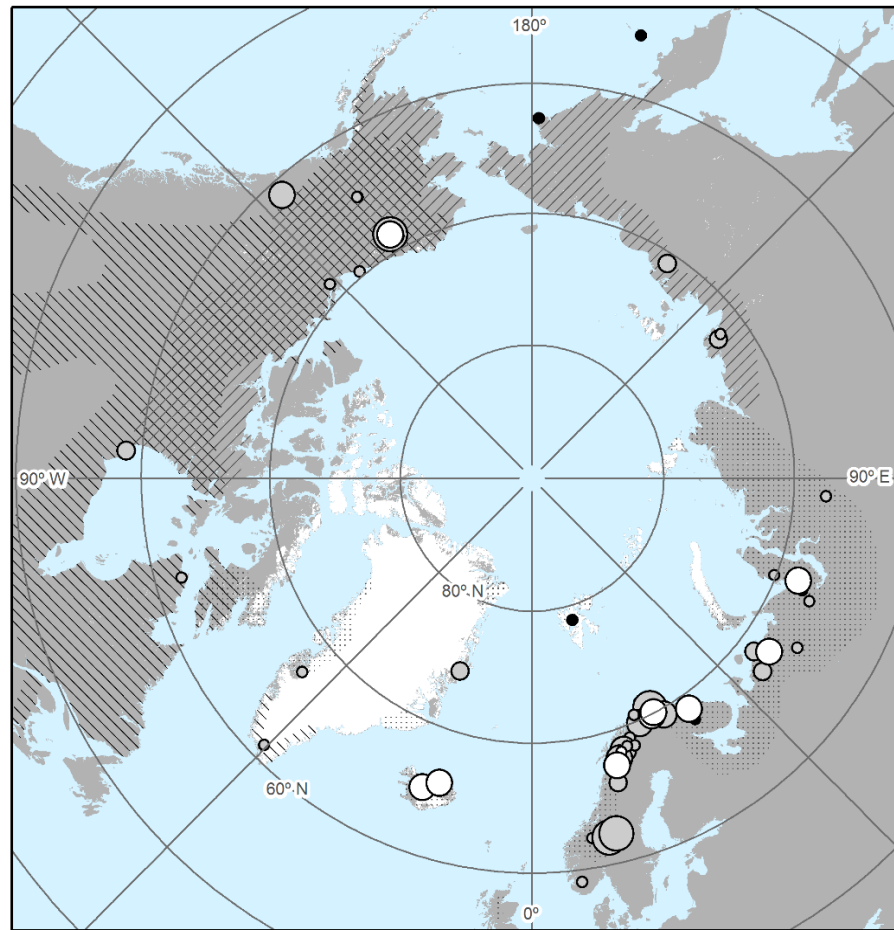
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592 **Figure 2.** Relationships between the intensity of total background invertebrate herbivory and July temperatures
593 (a,b) and precipitation (c,d): predicted values (sizes of data points are proportional to the number of samples at
594 each location), fitted lines and 95% confidence intervals. The intensity of herbivory was measured as the
595 percentage of leaves damaged by invertebrates (a,c) and the percentage of leaf area affected out of all leaves
596 examined (b,d). Dashed vertical line indicate mean observed July temperature and precipitation values across
597 sites, and the box around them represents the range over which the absolute increases in herbivory were
598 calculated (1°C in a and b, 10 mm in c and d).
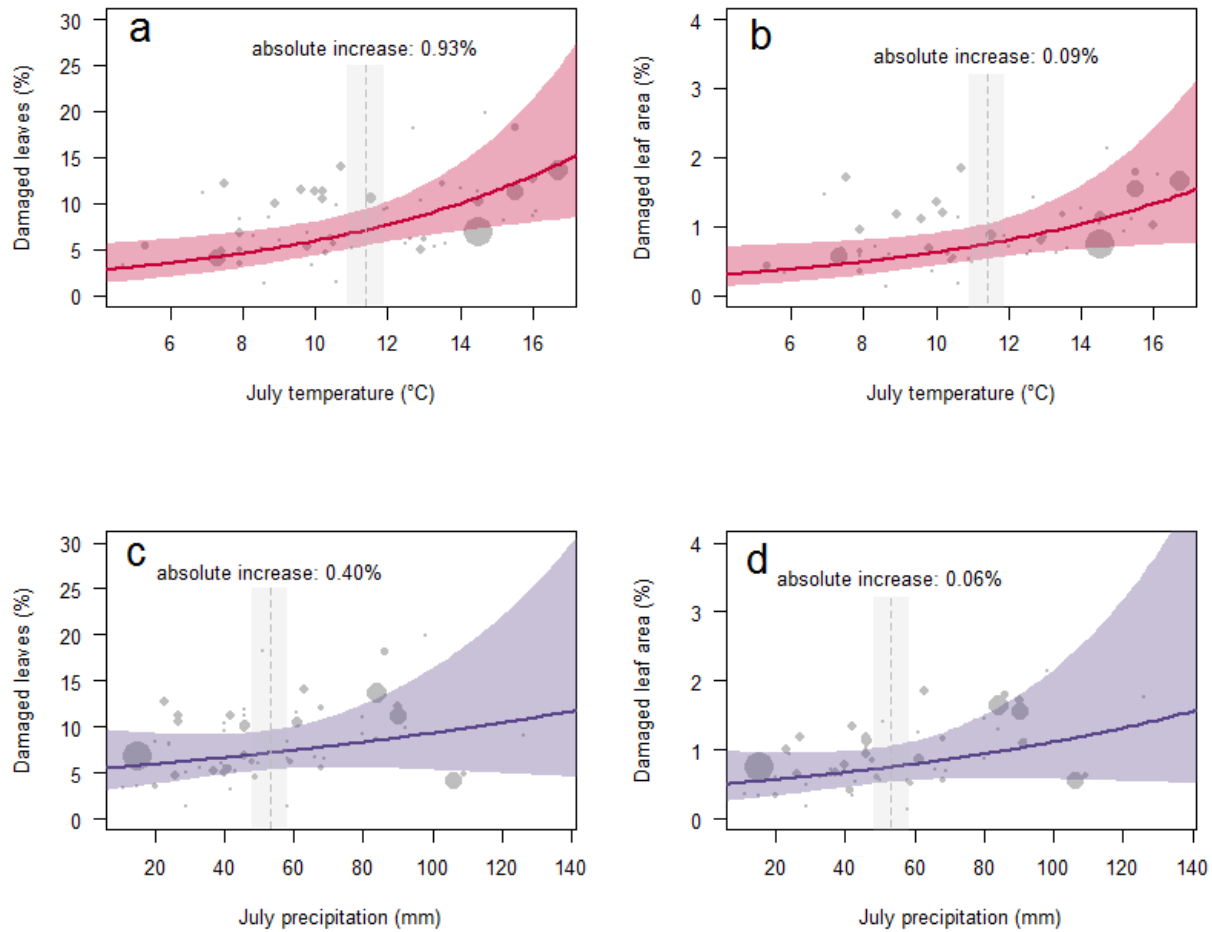
599

600 **Table 1.** Summary of sampling protocols, indicating the aim of the protocol and where it can be found, the dwarf
601 birch taxa targeted and the number of sampling locations and sites where samples were collected across locations.
602 Note that some of the 56 study areas were sampled in different years and/or targeted different dwarf birch taxa,
603 and are kept as separate 'sampling locations', so the number of locations presented in the table exceeds the
604 number of study areas. For more details on each location see Online Resource S2.

Protocol	Aim of protocol and accessibility	Dwarf birch taxon	Number of locations (sites)
2008-2013	Measure insect herbivory at the global scale. Available as Online Resource S2 to Kozlov et al. 2015b.	*Betula nana exilis*	2(2)
		Betula nana nana	7(7)
2014	Determine the level of anti-browsing defence in dwarf birch across the Arctic. This protocol was not aimed at measuring invertebrate herbivory. Only one of the samples collected in 2014, consisting of top shoots (both long and short shoots) of Betula, was used in the present study. The protocol is available in Online Resource S1 (this study).	*Betula glandulosa*	8(18)
		Betula nana exilis	6(20)
		Betula nana nana	29(99)
2015	Assess variability of background invertebrate herbivory in tundra at the plant community level. Only the results for dwarf birch were used in the present study. The protocol is available at: http://herbivory.biology.ualberta.ca/files/2016/11/background_herbivory_tundra.pdf	*Betula nana exilis*	1(5)
		Betula nana nana	9(41)
Total			62(192)

605

606

607 **Table 2.** Factors explaining variation in different measures of foliar damage in dwarf birch (Linear Mixed Effect
608 Model results) by all herbivores (a) and only defoliators (b), based on 62 samples from 56 locations across the
609 tundra biome (some locations were sampled in different years or targeted different *Betula* taxa (see Table 1) and
610 these locations are kept separate in the analyses). Baseline for species comparisons is *Betula nana* subsp. *nana*.
611 The percentage of leaves affected and leaf area affected were log-transformed before analyses. Estimates in bold
612 indicate that 95% confidence interval does not include zero. Sampling protocol was included as a random effect in
613 the models, and sample sizes at each location were included as weights. Random effects are presented as
614 standard deviations; n indicates the number of sampling protocols, and % refer to the percentage of residual
615 variance assigned to sampling protocol.

a. All herbivores						
Explanatory variables	Percentage of leaves damaged		Percentage of leaf area damaged		Area damaged per damaged leaf	
Fixed effects	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Intercept	**-2.993**	**-5.864, -0.122**	-2.460	-5.989, 1.069	40.419	-5.593, 86.432
Latitude	0.031	-0.002, 0.064	0.022	-0.018, 0.063	-0.246	-0.781, 0.288
Temperature	**0.051**	**0.016, 0.086**	**0.053**	**0.010, 0.096**	-0.050	-0.601, 0.501
Precipitation	**0.005**	**0.002, 0.009**	**0.006**	**0.001, 0.011**	0.022	-0.040, 0.085
Species – *B. glandulosa*	0.289	-0.067, 0.646	0.179	-0.259, 0.618	-2.629	-8.322, 3.063
Species – *B. n. exilis*	-0.254	-0.562, 0.054	-0.258	-0.637, 0.120	0.570	-4.362, 5.502
Collection date	0.004	-0.002, 0.010	0.000	-0.007, 0.007	-0.056	-0.148, 0.037
Random effects	SD		SD		SD	
Sampling protocol	0.239	(n=3, 13.1%)	0.279	(n=3, 12.0%)	2.409	(n=3, 5.6%)
Residual	0.615		0.756		9.889	
b. Defoliators						
Explanatory variables	Percentage of leaves damaged		Percentage of leaf area damaged		Area damaged per damaged leaf	
Fixed effects	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Intercept	-2.847	-5.724, 0.029	-2.468	-6.008, 1.071	37.042	-9.318, 83.042
Latitude	0.030	-0.004, 0.063	0.023	-0.018, 0.064	-0.218	-0.756, 0.321
Temperature	**0.050**	**0.015, 0.085**	**0.051**	**0.008, 0.094**	-0.093	-0.644, 0.458
Precipitation	**0.005**	**0.001, 0.009**	**0.006**	**0.001, 0.011**	0.021	-0.041, 0.084
Species – *B. glandulosa*	0.271	-0.087, 0.628	0.169	-0.271, 0.608	-2.425	-8.148, 3.297
Species – *B. n. exilis*	-0.264	-0.573, 0.044	-0.295	-0.675, 0.084	-0.278	-5.245, 4.690
Collection date	0.004	-0.002, 0.010	0.000	-0.007, 0.007	-0.047	-0.140, 0.045
Random effects	SD		SD		SD	
Sampling protocol	0.233	(n=3, 12.5%)	0.266	(n=3, 10.9%)	2.124	(n=3, 4.3%)
Residual	0.616		0.759		9.971	

616

617

618 **Table 3.** Factors explaining variation in the percentage of leaves damaged by leaf miners (a) and gall makers (b) on
619 dwarf birch (Linear Mixed Effect Model results), based on 62 samples from 56 locations across the tundra biome.
620 Baseline for species comparisons is *Betula nana* subsp. *nana*. The percentage of leaves affected was log-
621 transformed before analyses. Estimates in bold indicate that 95% confidence interval does not include zero.
622 Sampling protocol was included as a random effect in the models, and sample sizes at each location were included
623 as weights. Random effects are presented as standard deviations; n indicates the number of sampling protocols,
624 and % refer to the percentage of residual variance assigned to sampling protocol.
625

Explanatory variables	a. Leaf miners		b. Gall makers	
Fixed effects	Estimate	95% CI	Estimate	95% CI
Intercept	**-7.465**	**-12.596, -2.334**	-1.587	-6.252, 3.078
Latitude	0.035	-0.024, 0.094	0.008	-0.046, 0.062
Temperature	0.034	-0.021, 0.089	0.013	-0.040, 0.066
Precipitation	**0.009**	**0.002, 0.016**	0.005	-0.001, 0.012
Species – *B. glandulosa*	-0.167	-0.782, 0.448	**0.702**	**0.134, 1.270**
Species – *B. n. exilis*	-0.108	-0.656, 0.439	0.357	-0.142, 0.856
Collection date	**0.014**	**0.004, 0.023**	-0.006	-0.015, 0.003
Random effects	SD		SD	
Sampling protocol	0.000	(n=3, 0%)	0.112	(n=3, 1.2%)
Residual	1.107		1.005	

626