

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

3 Isabel C BARRIO^{1*}, Elin LINDÉN², Mariska TE BEEST², Johan OLOFSSON², Adrian ROCHA³, Eeva M
4 SOININEN⁴, Juha M ALATALO⁵, Tommi ANDERSSON⁶, Ashley ASMUS⁷, Julia BOIKE⁸, Kari Anne BRÅTHEN⁴,
5 John P BRYANT⁹, Agata BUCHWAL^{10,11}, C Guillermo BUENO¹², Katherine S CHRISTIE¹³, Yulia V DENISOVA¹⁴,
6 Dagmar EGELKRAUT², Dorothee EHRICH⁴, LeeAnn FISHBACK¹⁵, Bruce C FORBES¹⁶, Maite GARTZIA¹⁷, Paul
7 GROGAN¹⁸, Martin HALLINGER¹⁹, Monique M P D HEIJMANS²⁰, David S HIK²¹, Annika HOFGAARD²²,
8 Milena HOLMGREN²³, Toke T HØYE²⁴, Diane C HUEBNER²⁵, Ingibjörg Svala JÓNSDÓTTIR^{1,26}, Elina
9 KAARLEJÄRVI^{2,27}, Timo KUMPULA²⁸, Cynthia Y M J G LANGE²⁹, Jelena LANGE³⁰, Esther LÉVESQUE³¹, Juul
10 LIMPENS²⁰, Marc MACIAS-FAURIA³², Isla MYERS-SMITH³³, Erik J van NIEUKERKEN³⁴, Signe NORMAND³⁵,
11 Eric S POST³⁶, Niels Martin SCHMIDT³⁷, Judith SITTERS^{2,38}, Anna SKORACKA³⁹, Alexander SOKOLOV^{40,41},
12 Natalya SOKOLOVA^{40,41}, James D M SPEED⁴², Lorna E STREET⁴³, Maja K SUNDQVIST^{2,44}, Otso SUOMINEN⁶,
13 Nikita TANANAEV⁴⁵, Jean-Pierre TREMBLAY⁴⁶, Christine URBANOWICZ⁴⁷, Sergey A UVAROV⁴⁸, David
14 WATTS⁴⁹, Martin WILMKING³⁰, Philip A WOOKEY⁴², Heike H ZIMMERMANN⁸, Vitali ZVEREV⁵⁰, Mikhail V
15 KOZLOV⁵⁰

16 ¹Department of Life and Environmental Sciences, University of Iceland, Sturlugata 7 101 Reykjavík, Iceland

17 ²Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden

18 ³Department of Biological Sciences and the Environmental Change Initiative, University of Notre Dame, Notre Dame, IN 46556, USA

19 ⁴Department of Arctic and Marine Biology, UiT – The Arctic University of Norway, NO-9037, Tromsø, Norway

20 ⁵Qatar University, Department of Biological and Environmental Sciences, College of Arts and Sciences, Doha, Qatar

21 ⁶Kevo Subarctic Research Institute, Biodiversity Unit, University of Turku, FI-20014, Turku, Finland

22 ⁷Department of Biology, The University of Texas at Arlington, Arlington, Texas, USA

23 ⁸Alfred Wegener Institute for Polar and Marine Research, Telegrafenberg A43, 14473 Potsdam, Germany

24 ⁹Institute of Arctic Biology, University of Alaska Fairbanks, 997775-7000 Fairbanks, Alaska, USA

25 ¹⁰Adam Mickiewicz University, Institute of Geocology and Geoinformation, Dziegiełowa 21, 61-680 Poznań, Poland

26 ¹¹University of Alaska Anchorage, Department of Biological Sciences, 3151 Alumni Loop, 99508 Anchorage, Alaska, USA

27 ¹²Institute of Ecology and Earth Sciences, Department of Botany, University of Tartu, Lai 40, Tartu, 51005, Estonia

28 ¹³Science Department, Alaska SeaLife Center, 301 Railway Ave., 99664 Seward, Alaska, USA

29 ¹⁴Nenets Agrarian-Economic Technical School, Studencheskaya 1, 166000 Naryan-Mar, Russia.

30 ¹⁵Churchill Northern Studies Centre, PO Box 610, R0B 0E0 Churchill, Manitoba, Canada

31 ¹⁶Arctic Centre, University of Lapland, Box 122, FI-96101 Rovaniemi, Finland

32 ¹⁷Pyrenean Institute of Ecology (CSIC). Avda. Nuestra Señora de la Victoria s/n, 22700 Jaca, Spain

33 ¹⁸Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

34 ¹⁹Swedish Agricultural University, Ullsväg 16, 75651 Uppsala, Sweden

35 ²⁰Plant Ecology and Nature Conservation Group, Wageningen University & Research, Droevendaalsesteeg 3, NL-6708 PB
36 Wageningen, the Netherlands

37 ²¹Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T5N 0R5, Canada

38 ²²Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

39 ²³Resource Ecology Group, Wageningen University & Research, Droevendaalsesteeg 3, 6708 PB Wageningen, The Netherlands

40 ²⁴Arctic Research Centre and Department of Bioscience, Aarhus University, Grenåvej 14, DK-8410 Rønne, Denmark

41 ²⁵Department of Biology & Wildlife, University of Alaska Fairbanks, 982 N Koyukuk Drive, 101 Murie, 99775-6100 Fairbanks, USA

42 ²⁶University Centre in Svalbard (UNIS), Longyearbyen NO-9171, Norway

43 ²⁷Department of Biology, Vrije Universiteit Brussel (VUB), Pleinlaan 2, 1050 Brussels, Belgium

44 ²⁸Department of Geographical and Historical Studies, University of Eastern Finland, 80101 Joensuu, Finland

45 ²⁹Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

46 ³⁰Institute of Botany and Landscape Ecology, University Greifswald, 17487 Greifswald, Germany

47 ³¹Université du Québec à Trois-Rivières and Centre d'études nordiques, Trois-Rivières, Québec, G9A 5H7, Canada

48 ³²School of Geography & the Environment, University of Oxford, OX1 3QY Oxford, United Kingdom

49 ³³School of GeoSciences, King's Buildings, West Mains Road, University of Edinburgh, Edinburgh, EH9 3FF, United Kingdom

50 ³⁴Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, The Netherlands
51 ³⁵Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000
52 Aarhus C, Denmark
53 ³⁶Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, USA
54 ³⁷Arctic Research Centre, Department of Bioscience, Aarhus University, 4000 Roskilde, Denmark
55 ³⁸Ecology and Biodiversity, Department Biology, Vrije Universiteit Brussel, 1050 Brussels, Belgium
56 ³⁹Population Ecology Lab, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University in Poznań,
57 Umultowska 89, 61–614 Poznań, Poland
58 ⁴⁰Arctic Research Station, Institute of Plant and Animal Ecology, Ural Branch of Russian Academy of Sciences, Zelenaya Gorka
59 Str., 21, 629400, Labytnangi, Russia
60 ⁴¹Arctic Research Center of the Yamal-Nenets Autonomous District, Salekhard, Russia
61 ⁴²Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, 7491 Trondheim,
62 Norway
63 ⁴³Environmental Sciences, School of Life Sciences, Heriot-Watt University, Edinburgh EH14 4AS, UK
64 ⁴⁴The Center for Macroecology, Evolution and Climate, The Natural History Museum of Denmark, University of Copenhagen,
65 Universitetsparken 5, 2100 Copenhagen Ø, Denmark
66 ⁴⁵Melnikov Permafrost Institute, Siberian Branch, Russian Academy of Sciences, Yakutsk, Russia
67 ⁴⁶Department of Biology, Centre for Nordic Studies and Centre for Forest Research, Université Laval, G1V 0A6, Québec, QC,
68 Canada
69 ⁴⁷Department of Biological Sciences, Dartmouth College, Hanover, NH, USA
70 ⁴⁸Nenets Museum of Local History, Pobedy 5, 166000 Naryan-Mar, Russia
71 ⁴⁹Intercollege Graduate Degree Program in Ecology and Department of Biology, The Pennsylvania State University, University
72 Park, Pennsylvania 16802, USA
73 ⁵⁰Section of Ecology, Department of Biology, University of Turku, FI-20014, Turku, Finland
74
75 *corresponding author: ICB icbarrio@gmail.com
76

77 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

95 INTRODUCTION

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 (Metcalf 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).

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 galls), 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 \pm SE: $11.2 \pm 1.3\%$; median=
290 8.8%, $n=62$; **Online Resource S5**). On average, $1.4 \pm 0.2\%$ of leaf area was damaged at each location (median =
291 1.1%), and most damaged leaves were only slightly affected ($12.0 \pm 0.9\%$ 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 $11.09 \pm 1.26\%$ 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 $0.06 \pm 0.02\%$ and, when present, leaf
337 miners affected on average $11.77 \pm 3.05\%$ of leaf area. Galls were found on $0.08 \pm 0.05\%$ leaves per location, and
338 affected $35.78 \pm 8.29\%$ 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 (Kotaniemi 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

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450

451 **REFERENCES**

452 Agrawal A, Weber M (2015) On the study of plant defence and herbivory using comparative approaches: how important are
453 secondary plant compounds. *Ecol Lett* 18:985–991
454 Andrew NR, Hughes L (2005) Herbivore damage along a latitudinal gradient: relative impacts of different feeding guilds. *Oikos*
455 108:176–182
456 Anstett D, Ahern J, Glinos J, et al (2015) Can genetically based clines in plant defence explain greater herbivory at higher

457 latitudes? *Ecol Lett* 18:1376–1386
 458 Anstett DN, Naujokaitis-Lewis I, Johnson MTJ (2014) Latitudinal gradients in herbivory on *Oenothera biennis* vary according to
 459 herbivore guild and specialization. *Ecology* 95:2915–2923
 460 Anstett DN, Nunes KA, Baskett C, Kotanen PM (2016) Sources of controversy surrounding latitudinal patterns in herbivory and
 461 defense. *Trends Ecol Evol* 31:789–802
 462 Bale JS, Masters GJ, Hodkinson ID, et al (2002) Herbivory in global climate change research: direct effects of rising temperature
 463 on insect herbivores. *Glob Chang Biol* 8:1–16
 464 Barrio IC, Bueno CG, Hik DS (2016) Warming the tundra: reciprocal responses of invertebrate herbivores and plants. *Oikos*
 465 125:20–28
 466 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models using lme4. *J Stat Softw* 67:1–48
 467 Batzli GO, White RG, MacLean SF, et al (1980) The herbivore-based ecosystem. In: Brown J, Miller PC, Tieszen LL, Bunnell FL
 468 (eds) An arctic ecosystem: the coastal tundra at Barrow, Alaska. pp 335–410
 469 Birkemoe T, Bergmann S, Hasle TE, Klanderud K (2016) Experimental warming increases herbivory by leaf-chewing insects in an
 470 alpine plant community. *Ecol Evol* 6:6955–6962
 471 Björkman C, Berggren A, Bylund H (2011) Causes behind insect folivory patterns in latitudinal gradients. *J Ecol* 99:367–369
 472 Bret-Harte MS, Shaver GR, Zoerner JP, et al (2001) Developmental plasticity allows *Betula nana* to dominate tundra subjected
 473 to an altered environment. *Ecology* 82:18–32
 474 Bryant JP, Joly K, Chapin FS, et al (2014) Can antibrowsing defense regulate the spread of woody vegetation in arctic tundra?
 475 *Ecography (Cop)* 37:204–211
 476 Carmona D, Lajeunesse MJ, Johnson MT (2011) Plant traits that predict resistance to herbivores. *Funct Ecol* 25:358–367
 477 Carneiro MAA, Fernandes GW, De Souza OFF (2005) Convergence in the variation of local and regional species richness.
 478 *Neotrop Entomol* 34:547–553
 479 CAVM Team (2003) Circumpolar Arctic Region Bioclimate Subzones. Scale 1:7,500,000.
 480 Coley P, Aide T (1991) Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In: Price P,
 481 Lewinsohn T, Fernandes G, Benson W (eds) Plant-animal interaction: evolutionary ecology in tropical and temperate
 482 regions. Wiley, New York, USA, pp 25–49
 483 Cook BI, Smerdon JE, Seager R, Coats S (2014) Global warming and 21st century drying. *Clim Dyn* 43:2607–2627
 484 Danks H V (1986) Insect plant interactions in arctic regions. *Rev d'Entomologie du Québec* 31:52–75
 485 DeAngelis DL, Bryant JP, Liu R, et al (2015) A plant toxin mediated mechanism for the lag in snowshoe hare population recovery
 486 following cyclic declines. *Oikos* 124:796–805
 487 Elmendorf SC, Henry GHR, Hollister RD, et al (2012) Global assessment of experimental climate warming on tundra vegetation:
 488 heterogeneity over space and time. *Ecol Lett* 15:164–175
 489 Euskirchen ES, McGuire AD, Chapin FS, et al (2009) Changes in vegetation in Northern Alaska under scenarios of climate change,
 490 2003–2100: implications for climate feedbacks. *Ecol Appl* 19:1022–1043
 491 Feilberg J (1984) A phytogeographical study of South Greenland. Vascular plants. *Meddelelser om Grønland, Biosci vol* 15 70
 492 Fisher AE., Hartley S., Young M (1999) Behavioural responses of the leaf-chewing guild to the presence of *Eriocrania* mines on
 493 silver birch (*Betula pendula*). *Ecol Entomol* 24:156–162
 494 Graglia E, Julkunen-Tiitto R, Shaver GR, et al (2001) Environmental control and intersite variations of phenolics in *Betula nana* in
 495 tundra ecosystems. *New Phytol* 151:227–236
 496 Greyson-Gaito CJ, Barbour MA, Rodriguez-Cabal MA, et al (2016) Freedom to move: Arctic caterpillar (Lepidoptera) growth rate
 497 increases with access to new willows (Salicaceae). *Can Entomol* 148:673–682
 498 Haukioja E (1981) Invertebrate herbivory at tundra sites. In: Bliss LC, Heal OW, Moore JJ (eds) Tundra ecosystems: a
 499 comparative analysis. Cambridge University Press, New York, USA, pp 547–555
 500 Hiura T, Nakamura M (2013) Different mechanisms explain feeding type-specific patterns of latitudinal variation in herbivore
 501 damage among diverse feeding types of herbivorous insects. *Basic Appl Ecol* 14:480–488
 502 Hodkinson ID, Bird J (1998) Host-specific insect herbivores as sensors of climate change in Arctic and alpine environments. *Arct*
 503 *Alp Res* 30:78–83
 504 IPCC [Intergovernmental Panel on Climate Change] (2013) Climate change 2013: the physical science basis. Contribution of
 505 Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge
 506 University Press, Cambridge, UK and New York, US
 507 Jepsen JU, Biuw M, Ims RA, et al (2013) Ecosystem impacts of a range expanding forest defoliator at the forest-tundra ecotone.
 508 *Ecosystems* 16:561–575
 509 Jepsen JU, Hagen SB, Ims RA, Yoccoz NG (2008) Climate change and outbreaks of the geometrids *Operophtera brumata* and
 510 *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. *J Anim Ecol* 77:257–264
 511 Johnson MTJ, Rasmann S (2011) The latitudinal herbivory- defence hypothesis takes a detour on the map. *New Phytol* 191:589–
 512 592
 513 Kaukonen M, Ruotsalainen AL, Wali P, et al (2013) Moth herbivory enhances resource turnover in subarctic mountain birch
 514 forests? *Ecology* 94:267–272

515 Koponen S (1984) Abundance of herbivorous insects on dwarf birch near the treeline in Alaska. Reports Kevo Subarctic
516 Research Station 19:19–24

517 Kotanen PM, Rosenthal JP (2000) Tolerating herbivory: does the plant care if the herbivore has a backbone? *Evol Ecol* 14:537–
518 549

519 Kozlov MVM, Skoracka A, Zverev V, et al (2016) Two birch species demonstrate opposite latitudinal patterns in infestation by
520 gall-making mites in Northern Europe. *PLoS One* 11:e0166641

521 Kozlov M V. (2008) Losses of birch foliage due to insect herbivory along geographical gradients in Europe: a climate-driven
522 pattern? *Clim Change* 87:107–117

523 Kozlov M V., Lanta V, Zverev V, Zvereva EL (2015a) Global patterns in background losses of woody plant foliage to insects. *Glob*
524 *Ecol Biogeogr* 24:1126–1135

525 Kozlov M V., van Nieukerken EJ, Zverev V, Zvereva EL (2013) Abundance and diversity of birch-feeding leafminers along
526 latitudinal gradients in northern Europe. *Ecography* 36:1138–1149

527 Kozlov M V, Filippov BY, Zubrij NA, Zverev V (2015b) Abrupt changes in invertebrate herbivory on woody plants at the forest-
528 tundra ecotone. *Polar Biol* 38:967–974

529 Kozlov M V, Zvereva EL (2017) Background insect herbivory: impacts, patterns and methodology. In: Cánovas FM, Lüttge U,
530 Matyssek R (eds) *Progress in Botany*. vol 79. doi: 10.1007/124_2017_4

531 Lawrimore JH, Menne MJ, Gleason BE, et al (2011) An overview of the global historical climatology network monthly mean
532 temperature data set, version 3. *J Geophys Res* 116:D19121

533 Leckey EH, Smith DM, Nufio CR, Fornash KF (2014) Oak-insect herbivore interactions along a temperature and precipitation
534 gradient. *Acta Oecologica* 61:1–8

535 Lim JY, Fine PVA, Mittelbach GG (2015) Assessing the latitudinal gradient in herbivory. *Glob Ecol Biogeogr* 1–7

536 Metcalfe DB, Crutsinger GM, Kumordzi BB, Wardle DA (2016) Nutrient fluxes from insect herbivory increase during ecosystem
537 retrogression in boreal forest. *Ecology* 97:124–132

538 Moles AT, Bonser SP, Poore AGB, et al (2011) Assessing the evidence for latitudinal gradients in plant defence and herbivory.
539 *Funct Ecol* 25:380–388

540 Moreira X, Abdala-Roberts L, Parra-Tabla V, Mooney KA (2015) Latitudinal variation in herbivory: Influences of climatic drivers,
541 herbivore identity and natural enemies. *Oikos* 124:1444–1452

542 Myers-Smith IH, Elmendorf SC, Beck PSA, et al (2015) Climate sensitivity of shrub growth across the tundra biome. *Nat Clim*
543 *Chang.* 5:887–891

544 Myers-Smith IH, Forbes BC, Wilmsking M, et al (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research
545 priorities. *Environ Res Lett* 6:45509

546 Nykänen H, Koricheva J (2004) Damage-induced changes in woody plants and their effects on insect herbivore performance: a
547 meta-analysis. *Oikos* 104:247–268

548 Olofsson J, Beest M te, Ericson L (2013) Complex biotic interactions drive long-term vegetation dynamics in a subarctic
549 ecosystem. *Philos Trans R Soc London B* 368:20120486

550 Onoda Y, Westoby M, Adler PB, et al (2011) Global patterns of leaf mechanical properties. *Ecol Lett* 14:301–312

551 Parker TC, Sadowsky J, Dunleavy H, et al (2017) Slowed biogeochemical cycling in sub-arctic birch forest linked to reduced
552 mycorrhizal growth and community change after a defoliation event. *Ecosystems* 20: 316

553 Pennings SC, Ho C, Salgado CS, et al (2009) Latitudinal variation in herbivore pressure in Atlantic coast salt marshes. *Ecology*
554 90:183–195

555 Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. *Proc Natl Acad Sci U S*
556 *A* 105:12353–8

557 Prevéy J, Vellend M, Rürger N, et al (2017) Greater temperature sensitivity of plant phenology at colder sites: implications for
558 convergence across northern latitudes. *Glob Chang Biol*. doi: DOI: 10.1111/gcb.13619

559 R Development Core Team (2015) R: A language and environment for statistical computing.

560 Richardson SJ, Press MC, Parsons AN, Hartley SE (2002) How do nutrients and warming impact on plant communities and their
561 insect herbivores? A 9-year study from a sub-Arctic heath. *J Ecol* 90:544–556

562 Roy BA, Gusewell S, Harte J (2004) Response of plant pathogens and herbivores to a warming experiment. *Ecology* 85:2570–
563 2581

564 Sinclair RJ, Hughes L (2008) Incidence of leaf mining in different vegetation types across rainfall, canopy cover and latitudinal
565 gradients. *Austral Ecol* 33:353–360

566 Speed JD, Austrheim G, Hester AJ, Mysterud A (2011) Browsing interacts with climate to determine tree-ring increment. *Funct*
567 *Ecol* 25:1018–1023

568 Speed JDM, Austrheim G, Hester AJ, Mysterud A (2013) The response of alpine *Salix* shrubs to long-term browsing varies with
569 elevation and herbivore density. *Arctic, Antarct Alp Res* 45:584–593

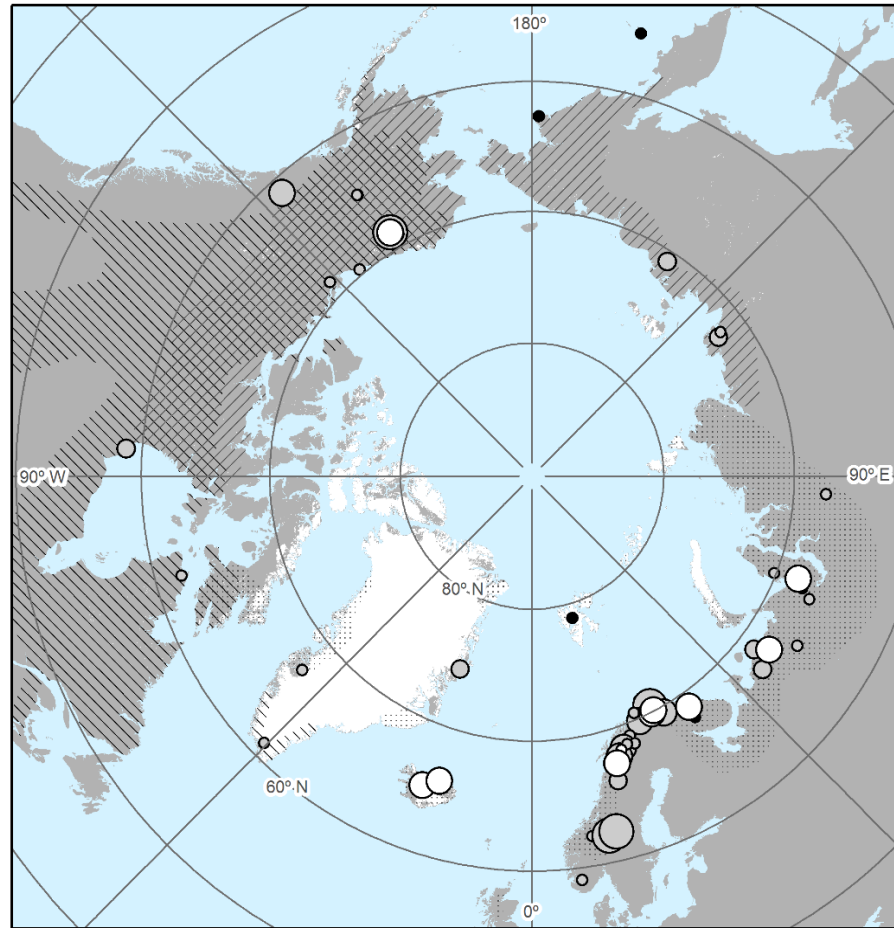
570 Stark S, Väisänen M, Yläne H, et al (2015) Decreased phenolic defence in dwarf birch (*Betula nana*) after warming in subarctic
571 tundra. *Polar Biol* 38:1993–2005

572 Torp M, Witzell J, Baxter R, Olofsson J (2010) The effect of snow on plant chemistry and invertebrate herbivory: experimental

573 manipulations along a natural snow gradient. *Ecosystems* 13:741–751
574 Viramo J (1962) Über die an der Zwergbirke (*Betula nana* L.) minierenden Insektenarten. *Ann Entomol Fenn* 28:118–126
575 Wilf P, Labandeira CC (1999) Response of plant-insect associations to Paleocene-Eocene warming. *Science* 284:2153–2156
576 Wilf P, Labandeira CC, Johnson KR, et al (2001) Insect herbivory, plant defense and early Cenozoic climate change. *Proc Natl*
577 *Acad Sci* 98:6221–6226
578 Wolf A, Kozlov M V, Callaghan T V (2008) Impact of non-outbreak insect damage on vegetation in northern Europe will be
579 greater than expected during a changing climate. *Clim Chang* 87:91–106
580 Zhang S, Zhang Y, Ma K, Shefferson R (2016) Latitudinal variation in herbivory: hemispheric asymmetries and the role of climatic
581 drivers. *J Ecol* 104:1089–1095
582 Zuur AF, Ieno EN, Walker NJ, et al (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York
583 Zvereva EL, Zverev V, Kozlov M V. (2012) Little strokes fell great oaks: minor but chronic herbivory substantially reduces birch
584 growth. *Oikos* 121:2036–2043
585

586 **FIGURES**

587 **Figure 1.** Sampling locations across the tundra biome. Size of points indicates number of sites per location, and
588 colour indicates sampling protocol used: 2008-2013 (black), 2014 (grey) or 2015 (white). Distribution of dwarf birch
589 taxa is indicated after Bryant et al. (2014).



Number of samples per location

- 1-2
- 3-4
- 5-6
- 7-16

Sampling protocol

- 2008-2013 protocol
- 2014 protocol
- 2015 protocol

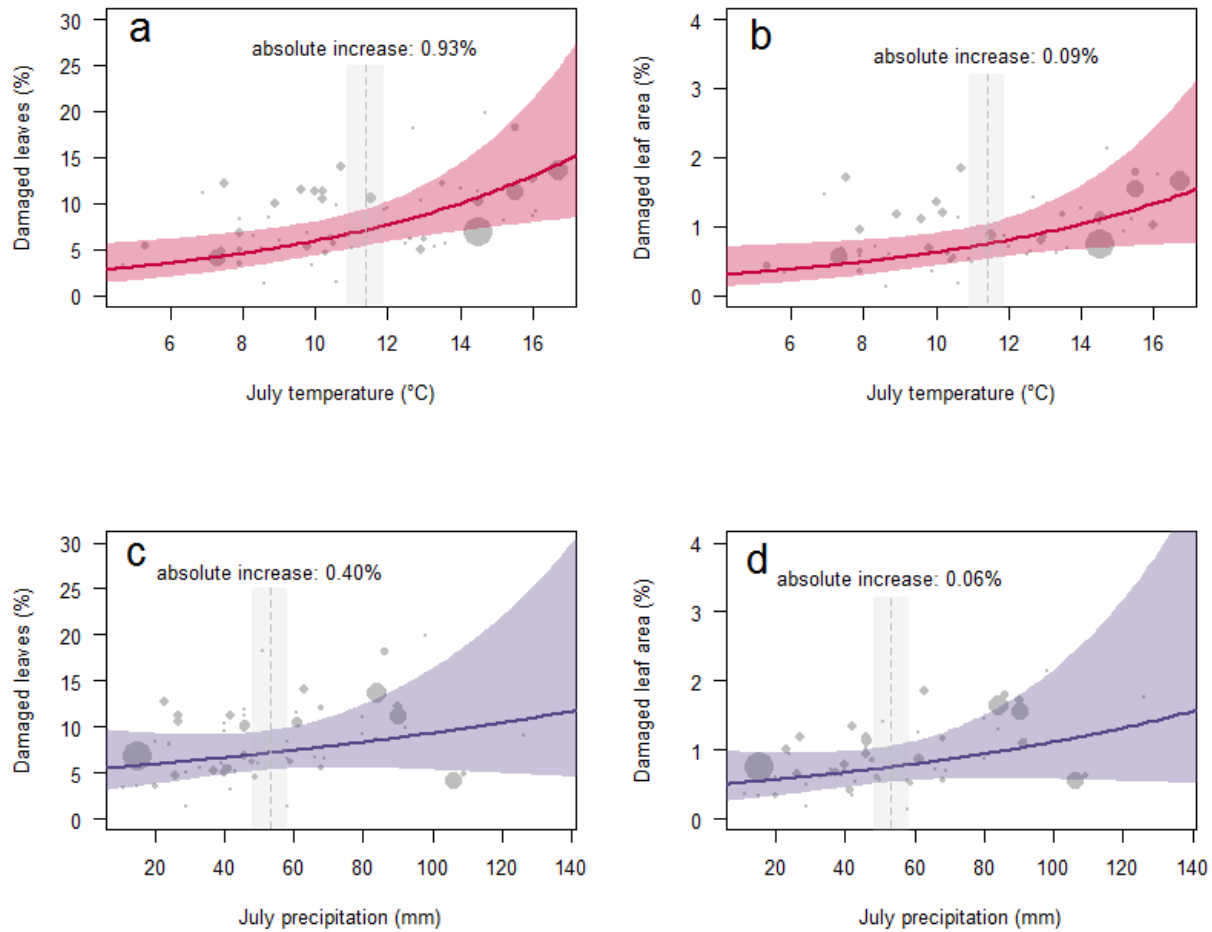
Dwarf birch taxa distribution

- *Betula nana nana*
- /// *Betula nana exilis*
- /// *Betula glandulosa*

590

591

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.	<i>Betula nana exilis</i>	2(2)
		<i>Betula nana nana</i>	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 <i>Betula</i> , was used in the present study. The protocol is available in Online Resource S1 (this study).	<i>Betula glandulosa</i>	8(18)
		<i>Betula nana exilis</i>	6(20)
		<i>Betula nana nana</i>	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	<i>Betula nana exilis</i>	1(5)
		<i>Betula nana nana</i>	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	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
<i>Fixed effects</i>						
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 – <i>B. glandulosa</i>	0.289	-0.067, 0.646	0.179	-0.259, 0.618	-2.629	-8.322, 3.063
Species – <i>B. n. exilis</i>	-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
<i>Random effects</i>	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	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
<i>Fixed effects</i>						
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 – <i>B. glandulosa</i>	0.271	-0.087, 0.628	0.169	-0.271, 0.608	-2.425	-8.148, 3.297
Species – <i>B. n. exilis</i>	-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
<i>Random effects</i>	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	
	Estimate	95% CI	Estimate	95% CI
<i>Fixed effects</i>				
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 – <i>B. glandulosa</i>	-0.167	-0.782, 0.448	0.702	0.134, 1.270
Species – <i>B. n. exilis</i>	-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
<i>Random effects</i>	SD		SD	
Sampling protocol	0.000	(n=3, 0%)	0.112	(n=3, 1.2%)
Residual	1.107		1.005	

626