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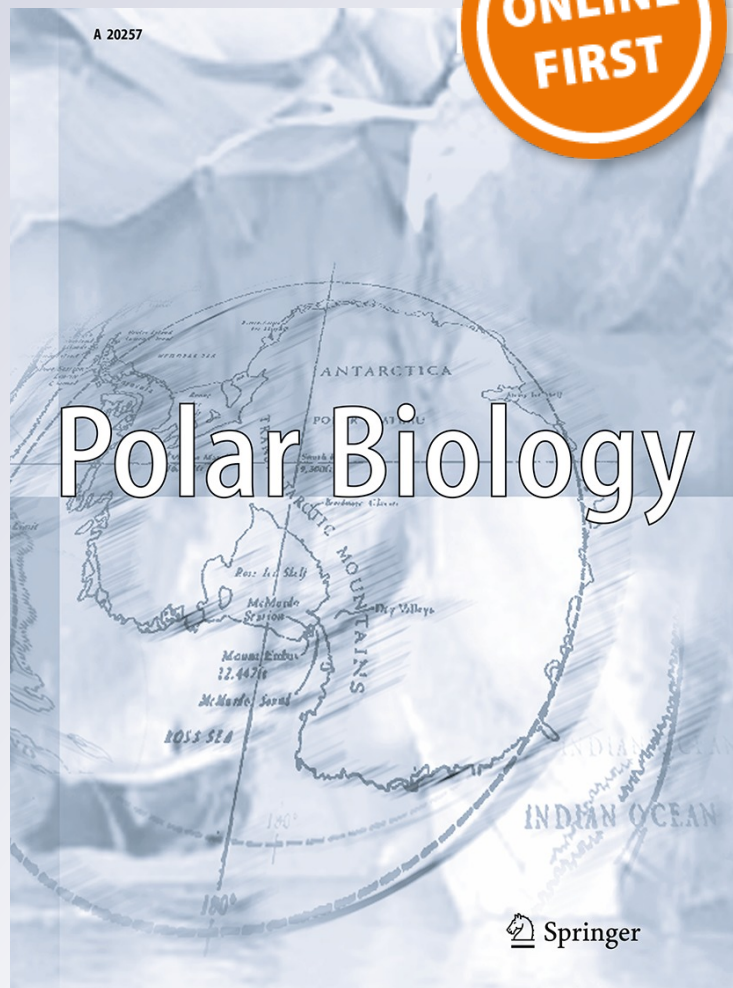
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Background invertebrate herbivory on dwarf birch (*Betula glandulosa-nana* complex) increases with temperature and precipitation across the tundra biome

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Abstract Chronic, low intensity herbivory by invertebrates, termed background herbivory, has been understudied in tundra, yet its impacts are likely to increase in a warmer Arctic. The magnitude of these changes is however hard to predict as we know little about the drivers of cur-

rent levels of invertebrate herbivory in tundra. We assessed the intensity of invertebrate herbivory on a common tundra plant, the dwarf birch (*Betula glandulosa-nana* complex), and investigated its relationship to latitude and climate across the tundra biome. Leaf damage by defoliating, mining and gall-forming invertebrates was measured in samples collected from 192 sites at 56 locations. Our results indicate that invertebrate herbivory is nearly ubiquitous across the tundra biome but occurs at low intensity. On average, invertebrates damaged 11.2% of the leaves and removed 1.4% of total leaf area. The damage was

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mainly caused by external leaf feeders, and most damaged leaves were only slightly affected (12% leaf area lost). Foliar damage was consistently positively correlated with mid-summer (July) temperature and, to a lesser extent, precipitation in the year of data collection, irrespective of latitude. Our models predict that, on average, foliar losses to invertebrates on dwarf birch are likely to increase by 6–7% over the current levels with a 1 °C increase in summer temperatures. Our results show that invertebrate herbivory on dwarf birch is small in magnitude but given its prevalence and dependence on climatic variables, background invertebrate herbivory should be included in predictions of climate change impacts on tundra ecosystems.

Keywords Background insect herbivory · Climate change · Externally feeding defoliators · Latitudinal Herbivory Hypothesis · Leaf damage · Leaf miners · Gall makers · Macroecological pattern

Introduction

The role of invertebrate herbivores in tundra ecosystems has been understudied (Haukioja 1981). Admittedly, the proportion of herbivorous taxa among invertebrates is lower in Arctic regions than at lower latitudes (Danks 1986), and invertebrate herbivores generally occur at relatively low abundances in tundra (Haukioja 1981). However, outbreaks of invertebrate herbivores have been well documented in the forest-tundra ecotone (Jepsen et al.

2008; Kaukonen et al. 2013) and occasionally in tundra (Post and Pedersen 2008). These massive defoliation events have large impacts on subarctic birch forests, enhancing resource turnover through deposition of frass and carcasses to the soil (Kaukonen et al. 2013) and causing vegetation shifts from forested to open conditions with consequences for ecosystem functioning and trophic interactions (Jepsen et al. 2013; Olofsson et al. 2013; Parker et al. 2017). In contrast, chronic leaf consumption by invertebrate herbivores when they occur at low densities, termed background herbivory (Kozlov and Zvereva 2017), has long been assumed to be unimportant, especially in the Arctic (Batzli et al. 1980; Haukioja 1981). However, recent studies in boreal forest indicate that chronic invertebrate herbivory can have stronger impacts on plant growth in the long term than infrequent bouts of severe damage (Zvereva et al. 2012), and can play a major role in ecosystem-level nutrient cycling (Metcalf et al. 2016). Yet, the extent, drivers and consequences of background herbivory across the tundra biome remain unquantified (Kozlov et al. 2015b).

The Latitudinal Herbivory Hypothesis (LHH) suggests that the intensity of herbivory should decrease with increasing latitude (Coley and Aide 1991; Johnson and Rasmann 2011). In its original formulation, it was argued that a wider diversity of specialist herbivores in tropical areas, together with warmer temperatures and a longer growing season, could lead to increased herbivory rates at lower latitudes. Empirical evidence has found support for LHH at the global scale, demonstrating that invertebrate herbivory of woody plants is generally lower in the polar

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regions than in temperate and tropical zones (Kozlov et al. 2015a). However, the generality of the LHH across plant functional types, invertebrate species and spatial scales is still debated (Moles et al. 2011; Anstett et al. 2016; Zhang et al. 2016). Latitudinal patterns with increased levels of herbivory at lower latitudes have been described for some species of plants and groups of insect herbivores (Kozlov 2008; Pennings et al. 2009; Moreira et al. 2015; Kozlov et al. 2016), but lack of latitudinal trends (Andrew and Hughes 2005; Kozlov 2008; Pennings et al. 2009), higher levels of herbivory at higher latitudes (Moreira et al. 2015; Kozlov et al. 2016) or even dome-shaped patterns (Kozlov et al. 2015a) have been described for others. Moreover, such studies have typically been conducted in temperate regions; whether latitudinal patterns can be found within the tundra biome remains unknown. Similarly, the mechanisms behind these macroecological patterns in background herbivory are poorly understood. Biotic and abiotic factors vary with latitude and this variability may promote variation in herbivory. For example, it has been suggested that, along with direct effects of climate, latitudinal gradients in herbivory may be shaped by changes in plant defensive chemistry (Moles et al. 2011), in predator pressure (Björkman et al. 2011) or by variations in leaf toughness (Onoda et al. 2011).

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

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

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invertebrate herbivory will also be influenced by climatic gradients in this region.

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

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

The objective of this study is to assess the intensity of background invertebrate herbivory and characterise its relationships with latitude and climatic variables in tundra. To achieve this goal, we measured leaf damage by tissue-feeding invertebrate herbivores on a common tundra plant with a circumpolar distribution, the dwarf birch (*Betula glandulosa-nana* complex), across a large number of sites spanning nearly 24° of latitude. Dwarf birch is a main food plant of many tundra herbivores (Koponen 1984; Bryant et al. 2014) and it is an important component in shrub

tundra plant communities. The wide distribution of dwarf birch facilitates comparisons within a single host plant across a latitudinal gradient (Anstett et al. 2016); further, the range and abundance of dwarf birch are predicted to expand in response to warming (Euskirchen et al. 2009; Myers-Smith et al. 2011). We test the following hypotheses: (1) background invertebrate herbivory within the tundra biome is greatest at lower latitudes, consistent with the LHH, or where summer temperature and precipitation are highest; and (2) the patterns of invertebrate herbivory by different feeding guilds will correspond with different climatic variables, given their sensitivity to different environmental cues. Specifically, we expect leaf damage by externally feeding defoliators to be more strongly associated with summer temperature than damage by internally feeding herbivores (leaf miners and gallers), and conversely that the latter will be more affected by climatic variables that determine leaf toughness, such as precipitation.

Methods

Focal plant species and leaf sampling

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

Plant material was collected in the summers of 2008–2013 (summarized by Kozlov et al. 2015b), 2014 and 2015 between June 12 and September 17. Although different protocols were followed in different years (Table 1), samples were collected in a way that allowed for spatial comparisons to evaluate background herbivory and its

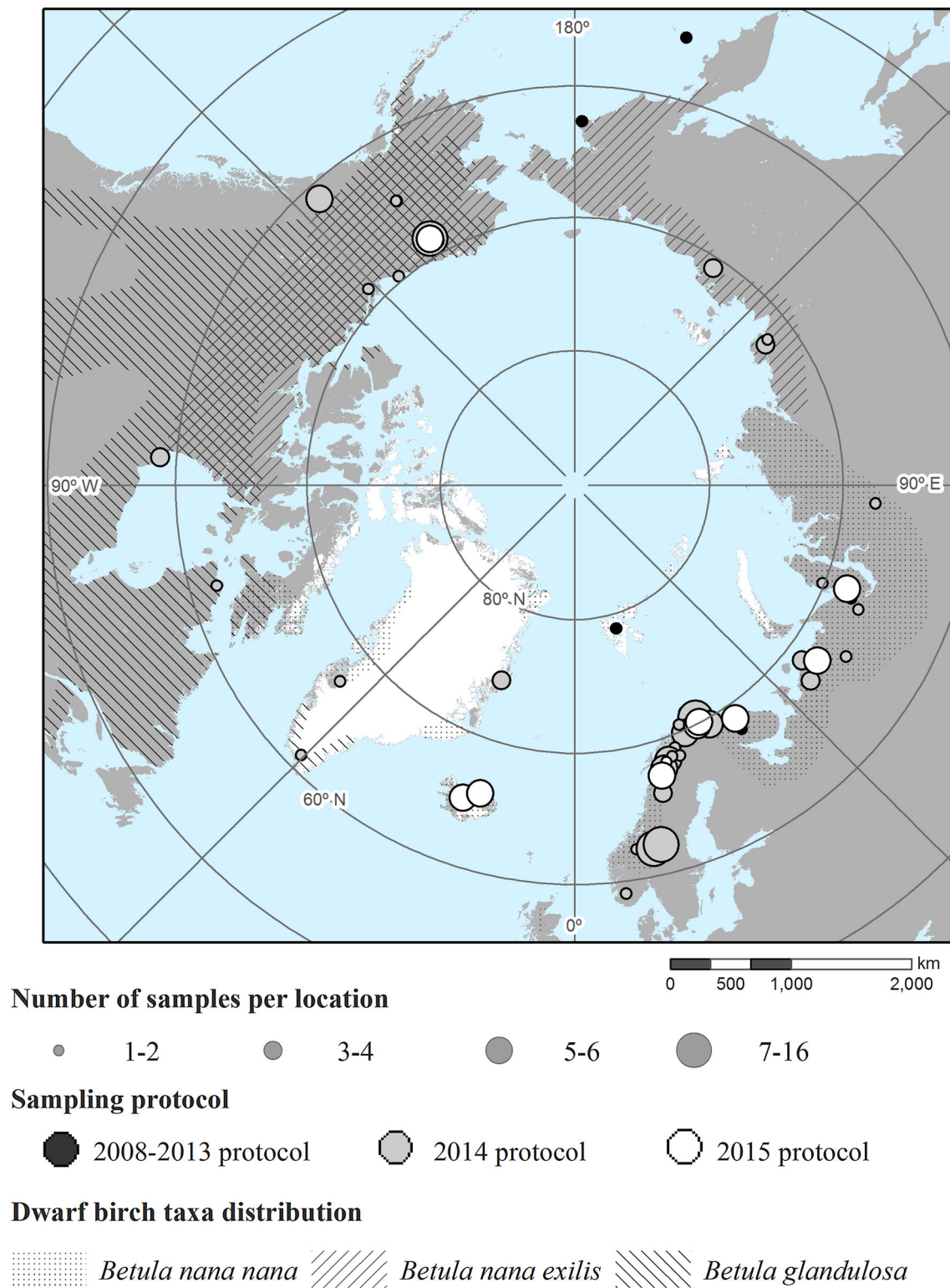


Fig. 1 Sampling locations across the tundra biome. Size of points indicates number of sites per location, and colour indicates sampling protocol used: 2008–2013 (black), 2014 (grey) or 2015 (white). Distribution of dwarf birch taxa is indicated after Bryant et al. (2014)

relationship to abiotic conditions. The protocol used in 2008–2013 (see Appendix S2 to Kozlov et al. 2015b) aimed at sampling plant foliage for measurements of insect herbivory at the global scale. The 2014 protocol was designed to assess defensive chemistry of dwarf birches across the Arctic (Online Resource S1); for the purpose of this study we only used one of the two top shoot samples collected in 2014 (both long and short shoots). We disregarded the samples specifically collected from short shoots (primary growth), as they may not be representative of herbivory on the whole plant. The 2015 protocol was aimed at measuring background invertebrate herbivory in tundra at the plant community level (http://herbivory.biology.ualberta.ca/files/2016/11/background_herbivory_tundra.pdf); here we report only the results for dwarf birch.

Briefly, all sampling protocols requested collection of birch leaves from several individuals per site (2–5 individuals were sampled in 2008–2013, ten individuals in 2014, and three individuals in 2015). The samples included 71–500 leaves per site, where sites were defined as circular areas of approximately 10 m radius, at least 100 m apart. The number of sites within a location (i.e., spatially distinct ‘study areas’, at least 10 km apart) varied between 1 and 16 (for the 2008–2013 and 2014 protocols, a minimum of one site per location was requested, while for the 2015 protocol, the minimum number of sites per location was five). Samples were collected from 192 sites in 56 locations (Table 1), spanning 23.7° of latitude across the tundra biome (including non-Arctic locations in alpine areas), from 55.2° N to 78.9° N (Fig. 1; Online Resource S2). The geographical distribution of locations was not designed in advance: the requests for sampling were distributed across

the research community, and all samples received were included in our study.

Leaf damage assessment

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

Following a widely used methodology (Kozlov and Zvereva 2017, and references therein), each leaf was assigned to a damage class according to the each type of damage (multiple damage types on the same leaf occurred in less than 1% of leaves analysed) and to the visually estimated percentage of the leaf area damaged by invertebrates: intact leaves, 0.01–1, 1–5, 5–25, 25–50, 50–75 and 75–100% (Kozlov 2008). Samples from the three protocols were evaluated by three scorers (2008–2013 protocol by MVK, 2014 by EL, 2015 by ICB); assessments made by the three scorers on 6–10 training samples (100

Table 1 Summary of sampling protocols, indicating the aim of the protocol and where it can be found, the dwarf birch taxa targeted and the number of sampling locations and sites where samples were collected

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)

Note that some of the 56 study areas were sampled in different years and/or targeted different dwarf birch taxa, and are kept as separate ‘sampling locations’, so the number of locations presented in the table exceeds the number of study areas

For more details on each location see Online Resource S2

leaves each) indicated no statistically significant effect of the scorer on the estimates of foliar damage (pairwise t test: all $p > 0.1$; intra-class correlation coefficients ranged between 0.56 and 0.88).

Data analysis

The intensity of invertebrate herbivory at each site was calculated using three complementary measures: (1) percentage of leaves damaged: the percentage of leaves that showed signs of invertebrate herbivory at a site; (2) percentage of leaf area damaged: the percentage of leaf area consumed or otherwise damaged by invertebrate herbivores over the total number of leaves inspected in a sample; and (3) average damage per damaged leaf: the average leaf area consumed or otherwise damaged by invertebrate herbivores per damaged leaf. The percentage of leaves damaged indicates the distribution of damage within a site; the percentage of leaf area damaged gives an approximation of foliar loss per site as a measure of herbivory; and the average damage per damaged leaf reflects how much of the leaf area is affected, once a leaf is damaged (Kozlov 2008; Kozlov et al. 2015b). To calculate the latter two variables, the number of leaves in each damage class was multiplied by the corresponding median value 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, 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 damage classes. These values were divided by the total number of leaves to obtain an estimate of the percentage of total leaf area damaged, and by the number of damaged leaves to obtain the average damage per damaged leaf (Kozlov et al. 2015a, b). All variables were calculated for all invertebrate herbivores and for the three different feeding guilds separately (Online Resource S2); given the low occurrence of mines and galls, only the percentage of leaves damaged was included in the models for these groups.

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

sampled at each location was included as weights in the models to account for differences in sampling effort.

We extracted the following indices as potential predictors of background herbivory: mean July temperature in the year of sampling, annual temperature, temperature seasonality (standard deviation of annual temperature), maximum temperature of the warmest month, minimum temperature of the coldest month, mean temp of warmest quarter (June–August), total July precipitation in the year of sampling, annual precipitation and precipitation seasonality (coefficient of variation). Initial correlation analyses indicated that mean July temperature and total July precipitation in the year of sampling had the highest correlations with measures of herbivory (Online Resource S4), so these two climate variables and latitude were included as predictors in the models. These two climate variables were extracted from the Global Historical Climatology Network-Monthly (GHCN-M v3.2.1, Lawrimore et al. 2011). This dataset provides monthly mean temperatures and precipitation as a spatial raster (0.5° resolution) based on weather station data. We extracted July temperature and precipitation for the year of sample collection, because current-season weather is more relevant to invertebrate herbivory than multi-year averages (Kozlov et al. 2013). Climate variables and latitude were included as predictors in the models. Correlations between continuous predictor variables were low ($r < 0.4$; Online Resource S4) and Variance Inflation Factors indicated no strong multicollinearity ($VIF < 1.2$), so all three variables were included simultaneously in the models. Dwarf birch exhibits patterns of regional and taxonomic variation in defence against browsing by vertebrates (Bryant et al. 2014) that may also affect the observed patterns of invertebrate herbivory, so we included dwarf birch taxon (*B. glandulosa*, *B. nana* ssp. *exilis* and *B. nana* ssp. *nana*) as a fixed effect variable in our analyses. We also included collection date, measured as day-of-year, as a fixed covariate in the models because foliar damage accumulates over the growing season, but damaged leaves tend to abscise prematurely (Torp et al. 2010; Kozlov et al. 2016). For the two locations where no invertebrate leaf damage was detected (Svalbard and Beringa Island), we assigned the lowest possible value for herbivory (0.1% for the percentage of leaves damaged by all herbivores and defoliators, 0.01% in the case of leaf miners and gallers, and 0.01% for leaf area damaged). The percentage of damaged leaves and the percentage leaf area affected by herbivory were then log-transformed to comply with model assumptions of normality and homogeneity of variances, which were checked by visually inspecting model residuals (Zuur et al. 2009). All analyses were run in R 3.2.3

(R Development Core Team 2015) using the *lme4* package to build linear mixed effects models (Bates et al. 2015).

Results

Feeding marks of invertebrate herbivores were found on 3949 of the 30,817 leaves examined (12.8%). Damage by invertebrate herbivores affected between 0 and 46.0% of leaves at each location (mean \pm SE: $11.2 \pm 1.3\%$; median = 8.8%, $n = 62$; Online Resource S5). On average, $1.4 \pm 0.2\%$ of leaf area was damaged at each location (median = 1.1%), and most damaged leaves were only slightly affected ($12.0 \pm 0.9\%$ of leaf area damaged;

median = 11.8%). The vast majority of damage (98.6%) was caused by defoliators. Damage by internally feeding herbivores (leaf miners and gallers) was found on relatively few leaves: 31 were mined by larvae of several moth species and only 24 bore galls (see Online Resource S6 for identification of mines and galls).

Total herbivory

Both the percentage of leaves with signs of invertebrate damage and the percentage of total leaf area damaged were positively associated with July temperature and precipitation (Table 2a), but there was no relationship with latitude. The models estimated linear increases of the log-

Table 2 Factors explaining variation in different measures of foliar damage in dwarf birch (linear mixed effect model results) by all herbivores (a) and only defoliators (b), based on 62 samples from 56

locations across the tundra biome (some locations were sampled in different years or targeted different *Betula* taxa (see Table 1) and these locations are kept separate in the analyses)

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
a. All herbivores						
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
Random effects	<i>SD</i>		<i>SD</i>		<i>SD</i>	
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						
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
Random effects	<i>SD</i>		<i>SD</i>		<i>SD</i>	
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	

Baseline for species comparisons is *Betula nana* ssp. *nana*

The percentage of leaves affected and leaf area affected were log-transformed before analyses

Estimates in bold indicate that 95% confidence interval does not include zero

Sampling protocol was included as a random effect in the models, and sample sizes at each location were included as weights

Random effects are presented as standard deviations; n indicates the number of sampling protocols, and % refers to the percentage of residual variance assigned to sampling protocol

transformed values of herbivory with increasing July temperature and precipitation (Table 2a), which implies smaller absolute increases in herbivory at locations with lower values of July temperature and precipitation, relative to locations with warmer and wetter summers (Fig. 2). For instance, the model estimates indicated a 0.4% absolute increase in the percentage of leaves damaged for every degree celsius increase in mean July temperature for the coldest mean July temperatures measured in our study (4.7 °C ; Fig. 2a). In contrast, the model estimates indicated a 1.7% absolute increase per degree celsius in the percentage of leaves damaged by invertebrate herbivores at locations with the highest mean July temperatures (16.7 °C ; Fig. 2a). Relative to current levels of herbivory (11.2% leaves damaged), these estimated values of absolute increase at locations with July temperature values within the centre of the observed temperature range (absolute increase 0.93%), represent relative increases in the percentage of leaves damaged of 8.3%. Similarly, the percentage of total leaf area damaged was estimated to

increase 0.04% per degree celsius in locations with colder summers and 0.17% per degree celsius in locations with warmer summers (Fig. 2b). Relative to observed current levels of leaf area damaged (1.4%), these figures imply predicted increases of 6.7% in leaf area damaged by invertebrate herbivores per degree C increase in mean July temperature, at locations with July temperature values within the centre of the observed temperature range (mean July temperature observed across sites = 11.4 °C).

The potential effects of increased precipitation followed similar trends, albeit a much weaker modelled effect than temperature. With a 10 mm increase in July precipitation, the percentage of leaves damaged by invertebrate herbivores increased by 0.3% in locations with the lowest observed precipitation (10.8 mm). In contrast, at locations with the highest observed mean July precipitation measured in our study (136.3 mm), the model estimated a 0.6% absolute increase in the percentage of leaves damaged (Fig. 2c); the increase in the percentage of leaf area damaged ranged between 0.05 and 0.12% in locations with

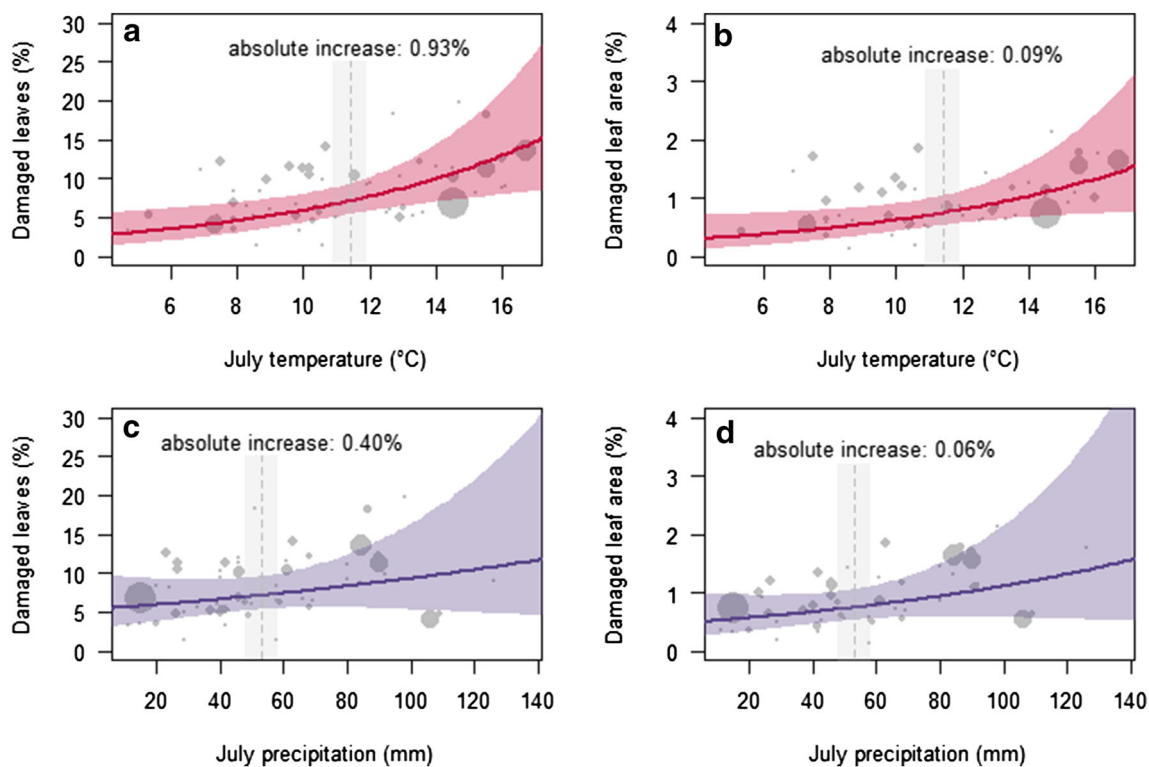


Fig. 2 Relationships between the intensity of total background invertebrate herbivory and July temperatures (a,b) and precipitation (c,d): predicted values (sizes of data points are proportional to the number of samples at each location), fitted lines and 95% confidence intervals. The intensity of herbivory was measured as the percentage of leaves damaged by invertebrates (a,c) and the percentage of leaf

area affected out of all leaves examined (b,d). Dashed vertical line indicate mean observed July temperature and precipitation values across sites, and the box around them represents the range over which the absolute increases in herbivory were calculated (1 °C in a and b, 10 mm in c and d)

drier and wetter summers (Fig. 2d). Relative to current levels of invertebrate herbivory, at sites with intermediate observed levels of July precipitation (mean total July precipitation observed across sites = 53.2 mm), the models predicted a 3.6% relative increase in the percentage of leaves damaged and 4.5% increase in percentage of leaf area damaged per 10 mm of increased precipitation.

None of the covariates (birch taxa or collection date) included in the models for total herbivory were associated with the percentage of leaves damaged at each location or with the percentage leaf area damaged (Table 2a). The average damage per damaged leaf was not associated with latitude, temperature, precipitation, collection date or birch taxa (Table 2a).

Externally feeding defoliators

The distribution of damage by free-living defoliators within a site, as measured with the percentage of leaves damaged was associated with higher July temperature and precipitation (Table 2b), but no latitudinal pattern was apparent. When looking at foliar loss, the percentage of leaf area affected by defoliators was positively, albeit weakly, related to July precipitation and temperature (Table 2b). None of the covariates explained variation in on the percentage of leaves damaged by defoliators at each location or the percentage of leaf area damaged (Table 2b). On average, defoliators consumed $11.09 \pm 1.26\%$ of leaf area on damaged leaves (median = 8.56%), and this value

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

Internally feeding herbivores (leaf miners and galls)

The mean percentage of leaves damaged by leaf miners at each location was $0.06 \pm 0.02\%$ and, when present, leaf 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 affected $35.78 \pm 8.29\%$ of the leaf area of damaged leaves (excluding two galled leaves with petiole galls). The percentage of leaves damaged by leaf miners increased with July precipitation and collection date (Table 3a), and the percentage of leaves damaged by galls was associated with birch taxa, with *B. glandulosa* having a greater percentage of leaves damaged compared to *B. nana* ssp. *nana* (Table 3b).

Discussion

Our study is the first to provide a quantitative analysis of background invertebrate herbivory across the tundra biome. Our analysis of leaf damage on a common tundra shrub in 56 locations across the circumpolar North showed that background invertebrate herbivory is nearly ubiquitous in tundra but occurs at low intensity. On average, invertebrate herbivores consumed 1.4% of leaf area of dwarf birch and affected 11.2% of leaves. The variation in

Table 3 Factors explaining variation in the percentage of leaves damaged by leaf miners (a) and gall makers (b) on dwarf birch (linear mixed effect model results), based on 62 samples from 56 locations across the tundra biome

Explanatory variables	a. Leaf miners		b. Gall makers	
	Estimate	95% CI	Estimate	95% CI
Fixed effects				
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
Random effects				
Sampling protocol	0.000	(<i>n</i> = 3, 0%)	0.112	(<i>n</i> = 3, 1.2%)
Residual	1.107		1.005	

Baseline for species comparisons is *Betula nana* ssp. *nana*

The percentage of leaves affected was log-transformed before analyses

Estimates in bold indicate that 95% confidence interval does not include zero

Sampling protocol was included as a random effect in the models, and sample sizes at each location were included as weights

Random effects are presented as standard deviations; *n* indicates the number of sampling protocols, and % refers to the percentage of residual variance assigned to sampling protocol

background invertebrate herbivory in tundra showed no latitudinal pattern, but both foliar losses to external feeders and the percentage of leaves damaged by internal leaf feeders were greater at sites with higher summer temperature and precipitation. Contrary to our expectations, all feeding guilds responded to the different climatic variables in a similar way.

General patterns of herbivory in our study were dominated by external feeding herbivores, which caused over 98% of the damage. Similar to previous studies in northern areas (Kozlov 2008; Kozlov et al. 2015b) and also in the fossil record (Wilf et al. 2001), the incidence of galls and leaf miners relative to that of defoliators was very small. Although previous studies suggested that different groups of herbivores may respond differently to climate variables (Leckey et al. 2014; Moreira et al. 2015), our results do not support this view for the tundra; rather, our findings suggest a generalized increase in herbivory by all feeding guilds with increased temperature and precipitation. Such positive associations with temperature have already been described for these three groups of herbivores in northern Europe (chewers, Kozlov et al. 2015a; leaf miners, Kozlov et al. 2013; galls, Kozlov et al. 2016). Similarly, studies in other ecosystems have also found increased herbivory with increased precipitation for leaf chewers (Kozlov 2008; Moreira et al. 2015), leaf miners (Leckey et al. 2014) and the occurrence of galls (Leckey et al. 2014).

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

The average damage per damaged leaf (12.1%) is comparable to previous studies (6.9%, Kozlov et al. 2015a). These relatively low levels suggest that herbivores shift their feeding sites after even low levels of damage, possibly as a result of decreases in leaf palatability in response to damage or as a strategy to avoid detection by natural enemies (Fisher et al. 1999; Greyson-Gaito et al. 2016). Reductions in leaf palatability may be related to the

production of secondary chemical compounds in response to herbivory (Nykänen and Koricheva 2004). In northern dwarf birch, the production of secondary compounds both as induced or constitutive anti-herbivore defence shows local and regional variation (Graglia et al. 2001; Torp et al. 2010). For example, local topography can influence patterns of foliar concentrations of nitrogen and phenolic compounds in *B. nana* ssp. *nana* through its effects on snow accumulation and plant phenology (Torp et al. 2010). This spatial variation in defensive chemistry of birch potentially accounts for the relatively constant values of damage on damaged leaves over a range of climatic conditions. However, concentrations of plant secondary metabolites appear to be poor predictors of the extent of plant damage caused by insects under natural conditions (Carmona et al. 2011). The use of broad metrics, such as total phenolics, to measure resistance against herbivores or comparisons across unrelated species may obscure the importance of secondary compounds (Agrawal and Weber 2015; Anstett et al. 2015). This topic deserves further investigation, especially considering that climate change will also affect the defensive chemistry of plants. For example, phenolic compounds are expected to decrease with increased temperature (Stark et al. 2015), but the response to warming might differ depending on what type and combination of secondary metabolites plants have (Graglia et al. 2001).

Our models predicted that changes in invertebrate herbivory in response to temperature and precipitation will differ along the range of climates sampled. It must be kept in mind that our approach represents a space-for-time substitution, where we infer changes in herbivory from locations with different climatic variables. Despite its limitations, this approach provides the best solution given the virtual lack of long-term trend data in patterns of invertebrate herbivory in tundra over time. Given that climate models project warming of 6–10 °C over the next 100 years (IPCC 2013), the influence of temperatures on invertebrate background herbivory could be important. According to the logarithmic relationship indicated by our models, increases in invertebrate herbivory in locations with higher summer temperatures would be more pronounced than at locations with colder summers. The effect of precipitation followed similar trends but was not as pronounced and did not differ as much between the ends of the precipitation gradient. Precipitation is predicted to increase in the Arctic as a result of climate change (Cook et al. 2014), so these modest increases could, however, also be important. Differential climate sensitivities to temperatures and/or soil moisture have been also described for the phenology (Prevéy et al. 2017), community composition (Elmendorf et al. 2012) and growth (Myers-Smith et al. 2015) of tundra plants. For example, the growth of tundra

shrubs was found to be more responsive to climate in wetter than in drier regions (Myers-Smith et al. 2015). Herbivory itself may also interact with climate to determine tundra plant performance. This has been observed for vertebrate herbivory in tundra (Speed et al. 2011, 2013) and suggested for invertebrate herbivores (Barrio et al. 2016). In addition, climate warming has been linked to increased growth (Bret-Harte et al. 2001) and decreased investment in defence of *B. nana* ssp. *nana* (Stark et al. 2015), so while invertebrate herbivory may be expected to increase in prevalence in a warmer climate, the net outcome of climate-herbivore-plant interactions is less certain.

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

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

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