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PLANT-MICROBE-ANIMAL INTERACTIONS – ORIGINAL RESEARCH

Increasing shrub damage by invertebrate herbivores in the warming and drying tundra of West Greenland

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Abstract

Rapid warming is predicted to increase insect herbivory across the tundra biome, yet how this will impact the community and ecosystem dynamics remains poorly understood. Increasing background invertebrate herbivory could impede Arctic greening, by serving as a top–down control on tundra vegetation. Many tundra ecosystems are also susceptible to severe insect herbivory outbreaks which can have lasting effects on vegetation communities. To explore how tundra-insect herbivore systems respond to warming, we measured shrub traits and foliar herbivory damage at 16 sites along a landscape gradient in western Greenland. Here we show that shrub foliar insect herbivory damage on two dominant deciduous shrubs, *Salix glauca* and *Betula nana*, was positively correlated with increasing temperatures throughout the first half of the 2017 growing season. We found that the majority of insect herbivory damage occurred in July, which was outside the period of rapid leaf expansion that occurred throughout most of June. Defoliators caused the most foliar damage in both shrub species. Additionally, insect herbivores removed a larger proportion of *B. nana* leaf biomass in warmer sites, which is due to a combination of increased foliar herbivory with a coinciding decline in foliar biomass. These results suggest that the effects of rising temperatures on both insect herbivores and host species are important to consider when predicting the trajectory of Arctic tundra shrub expansion.

Keywords Arctic · Top–down · Arthropods · Foliage · Temperature

Introduction

Effects of rising temperatures on insect herbivores are predicted to be pronounced in Arctic ecosystems (Bale et al. 2002; Deutsch et al. 2008), as northern regions continue to warm at twice the rate of the global average (Serreze and Barry 2011). Already, observed warming is impacting Arctic arthropod populations by altering community composition and food web dynamics (Rich et al. 2013; Koltz et al. 2018), and increasing regional insect densities and activity (Asmus et al. 2018b). Increases in Arctic insect activity can equate to more herbivory (Barrio et al. 2018; Rheubottom et al. 2019), as warmer temperatures can increasing the growth and survival rates of insects and potentially increase metabolic demands (Bale et al. 2002; Deutsch et al. 2008; Culler et al. 2015; Kozlov and Zvereva 2015). Longer summer periods can also increase arthropod thermal budgets, thereby accelerating life cycles or increasing voltinism, which could translate to greater total herbivory pressure throughout the growing season (Bale et al. 2002).

Potential increases in Arctic insect herbivory can serve as a critical top–down regulator to vegetation growth and ongoing tundra shrub expansion (Post and Pedersen 2008). Insect herbivores can serve as a top–down control on plant growth either through episodic outbreak events (pulse dynamic) or chronic ambient or background herbivory (press dynamic) (Jentsch and White 2019; Rheubottom et al. 2019). Some Arctic systems, most notably the forest-tundra ecotone of Fennoscandia and the tundra of western Greenland, are

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home to populations of outbreaking Lepidoptera that episodically remove large quantities of plant foliar biomass in a matter of weeks (Ruohomäki et al. 2000; Young et al. 2014; Prendin et al. 2019). In contrast to pulse outbreak events, background herbivory is always present in terrestrial ecosystems and may have prolonged effects on plant growth, community interactions, and nutrient flux; however, these impacts are poorly understood (Barrio et al. 2018; Rheubottom et al. 2019). Recent work in boreal systems suggests that background herbivory in northern ecosystems could impose stronger reductions in net primary production of woody plants than short-term outbreaks (Zvereva et al. 2012; Kozlov et al. 2015) as damage to leaf tissue can suppress photosynthesis and long-term plant productivity (Nabity et al. 2009). Therefore, studies of Arctic background herbivory are needed to assess this potentially important control on Arctic vegetation.

However, variations in vegetation phenology, growth form, and chemistry can become an indirect control on insect herbivory and ultimately can increase, mitigate, or even reverse potential arthropod physiological gains from a warming environment. For instance, plant leaf-out timing and elongation are sensitive to temperature, occurring only once thermal thresholds and light requirements are met, which may or may not coincide with insect phenology (Mjaaseth et al. 2005; Torp et al. 2010b; Sweet et al. 2014, 2015). If plant and insect phenology are not synchronized, some arthropods may miss a critical period of highly nutritious food when young budding leaves are high in nitrogen yet poorly defended by plant defensive compounds (Ayres 1993; Feeny 1970; Coley and Barone 1996). If insect herbivores miss this period of high-quality food, growth and metabolism could become constrained (Barrio et al. 2016). Additionally, warmer climate conditions might allow for vegetation overcompensation, where plants are able to recover from any potential herbivory losses by increased growth (Trumble et al. 1993). However, compensatory vegetation growth requires adequate nutrient and water availability so this might not be possible in plant–insect systems that are inherently resource-limited, such as those found in the Arctic. Individual plant species can also respond differently to environmental controls and herbivory pressure (Eskelinen 2008). Therefore, it is important to study a combined plant–herbivore system to understand how warming temperatures might, simultaneously, directly and indirectly, affect top–down herbivory controls on vegetation.

In this study, we explore how higher temperatures impact background insect herbivory damage on two dominant Arctic shrubs, both across the growing season and along a natural landscape gradient in West Greenland. We tracked foliar herbivory damage on two deciduous shrubs that are found across the circumpolar tundra biome, *Betula nana* and *Salix glauca,* and are both known to be hosts to several different species of herbivorous tundra arthropods (Post and Pedersen 2008; Barrio et al. 2018; Rheubottom et al. 2019). By focusing our attention on two shrub species, we aimed to identify how separate plant–herbivore systems might respond differently to environmental warming, despite belonging to a similar plant function type. We predicted that young leaves would be exposed to high levels of herbivory as expanding, immature foliage is likely to be highest in nutritional value (% Nitrogen) and vulnerability (limited chemical or structural defensive compounds) (Ayres and MacLean 1987; Coley 1983). Additionally, using a space-for-time study design across the thermal landscape gradient, we examined the effects of temperature on cumulative mid-summer insect herbivory damage. We considered three potential hypotheses regarding how increasing temperatures might impact insect shrub foliar damage: (1) no observed variation in foliar damage across the landscape (Mosbacher et al. 2013; Kozlov and Zvereva 2015), (2) sites located in warmer landscape positions will have higher amounts of damaged biomass from arthropod herbivores potentially due to increases in insect activity and metabolic demand (Barrio et al. 2018; Rheubottom et al. 2019), or (3) a smaller proportion of leaves are damaged by insects in warm sites due to shrub compensatory growth (i.e. larger shrubs or larger leaves) (Trumble et al. 1993).

Methods

Study area

This study was conducted in the shrub tundra of western Greenland, between the town of Kangerlussuaq and the margin of the Greenland Ice Sheet (Fig. 1a). The vegetation comprises a shrub-grassland system and is a part of the low-shrub tundra bioclimate (Walker 2000). The dominant vegetation comprises shrubs including dwarf birch (*B. nana subsp. nana*)*,* gray willow (*S. glauca*)*,* arctic blueberry (*Vaccinium uliginosum*) and Lapland rosebay (*Rhododendron lapponicum*) with interspersed populations of low-lying forbs and herbaceous graminoids. Long-term weather records from the Kangerlussuaq airport indicate a mean annual temperature of − 4.7 °C with mean annual precipitation of 157 mm (Finger Higgens et al. 2019). Additionally, this region is currently experiencing a rate of warming at ~ 0.5 °C per decade, with over 2 °C mean annual warming occurring from 1975 to 2018 (Finger Higgens et al. 2019).

We utilized a landscape gradient to explore the potential role of increasing temperatures on background insect herbivory damage on Arctic deciduous shrubs. Stretching from the margin of the Greenland Ice Sheet in the east to the waters of Sondre Stromfjord in the west, sites near the

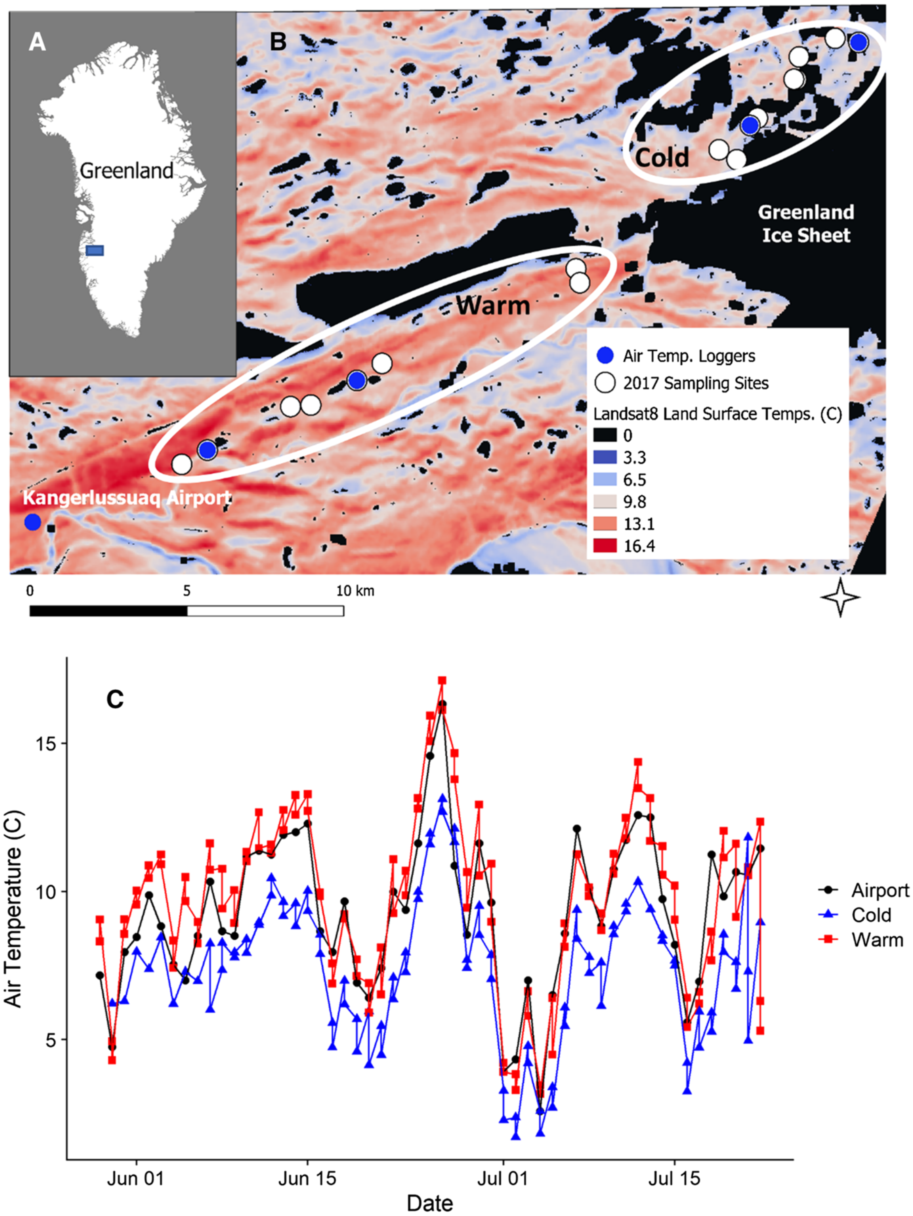

Fig. 1 Map of study region in West Greenland (blue box) (**a**) and seasonal air temperature variation along a landscape gradient.:and surface temperatures estimated from 12 June 2018 Landsat 8 Infrared Imagery (**b**) showing the locations of 16 monitoring sites (white dot) plus 5 ambient air temperature loggers (blue dot) with circled areas showing the separation of sites into "Warm" versus "Cold". Lower figure **c** shows seasonal variations in air temperature for the duration of data collection as recorded by the Kangerlussuaq airport (Danish Meteorological Institute), and averaged temperatures measured from 2 loggers with within "Cold" sites and "Warm" sites. Map first published in Finger Higgens et al. (2020)

ice sheet are approximately 3 °C cooler than sites near Kangerlussuaq (Bradley-Cook and Virginia 2018; Urbanowicz et al. 2018; Finger Higgens et al. 2020). This thermal gradient is largely driven by the cooling effects of the ice sheet and gains in altitude (from sea level to 660 m above sea level) that serve in combination to cool growing season air temperatures. Additionally, landscape variations in temperature and climate conditions are known to influence numerous ecological processes including soil carbon respiration (Bradley-Cook and Virginia 2018), soil wind erosion (Heindel et al. 2015), plant reproduction and pollinator interactions (Urbanowicz et al. 2018), and shrub growth form (Finger Higgens et al. 2020).

Site selection and air temperature modelling

From June 1 to July 27, 2017, 16 study sites at least 200 m distance from one another were established along the environmental gradient between Kangerlussuaq and the Greenland Ice Sheet (Fig. 1). Sites were selected in areas with a gentle slope (< 5°) and a mixed community of *B. nana* and *S. glauca* shrubs, covering an area of ~ 400 m^2. Half the sites (8) were closer to town and designated as "warm sites" while the other eight sites were located near the Greenland Ice Sheet and designated as "cold sites" (Fig. 1). Using a combination of remotely sensed land surface temperatures from Landsat 8 and five air temperature sensors (2 deployed Hobo Pendant Loggers at “colds sites”, 2 deployed Hobo Pendant Loggers at “warm sites (UA-002-64, Onset Computer Corp, Bourne, MA, USA, www.onsetcomp.com), and temperatures recorded at the Kangerlussuaq airport (DMI technical report 14-08, 18-08; http://research.dmi.dk/data/)), we estimated growing season air temperatures across our thermal gradient (Fig. 1; Finger Higgens et al. 2020). To interpolate the experienced temperatures at each of our study locations throughout the season, we created a regression model using the five recorded air temperatures (see above) and the remotely sense land surface temperatures from Landsat 8. Next, using this regression model, we modelled air temperatures for 12 June 2018, as this was a mid-season timepoint when all 16 study sites had an associated land surface temperature pixel value from available Landsat 8 data. Modelled air temperatures were later used as potential explanatory variables for regression models relating to foliar biomass damage.

Leaf elongation and leaf traits

In late May 2017, 10 shrubs that were a minimum of one m^3 approximately 3 m apart from one other of both *S. glauca* and *B. nana* were flagged for repeat sampling across the growing season at each of the 16 sites. From the flagged shrubs at all 16 sampling sites (10 *S. glauca* and *B. nana,* respectively), ~ 100 short shoot leaves per site (~ 10 per plant) were haphazardly removed and brought back to the laboratory for further analysis. Leaf samples were collected every 5 days in June and every 10 days in July until 19 July (for a total of 8 sampling periods), to monitor leaf expansion and area, leaf carbon and nitrogen, and to access herbivory damage. From each sampling date and from each sampling plot, leaves were pooled across all invididuals at each plot, and 20 randomly subsampled leaves per shrub species were scanned and processed with ImageJ software (Schneider et al. 2012) to calculate site-level average leaf area. The remaining collected leaves were air-dried for at least 14 days for future foliar nitrogen analyses, as percentage foliar N on a per weight basis, conducted on an ECS 4010 Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA) at Dartmouth College.

During a period of peak biomass (mid-July), estimates of vegetation biomass were conducted at all sites, using a point-frame intercept method as described in Finger-Higges et al. (2020) (Bråthen and Hagberg 2004; Barrio et al. 2018). Briefly, the point-frame method allows for the estimation of foliar biomass from the number of pin hits using established allometric equations. Point-frame estimates of foliar biomass ($g{\cdot}m^{-2}$) were conducted on four shrubs of both *B. nana* and *S. glauca* at each of the 16 study sites.

Herbivory damage assessments

Foliar herbivory was also assessed from early June to mid-July, 2017. Using leaves haphazardly collected from the field (see above), 20 leaves on each of the eight sampling dates were randomly selected for insect herbivore damage assessment, which involved visually examining both sides of each leaf with a light source and hand lens and prescribing a damage score. Herbivory scoring followed the protocol as described by the Herbivory Network (Barrio et al. 2018, 2021; Rheubottom et al. 2019), with the following damage classes: 0:no damage; 1:damage between 0.01 and 1%; 2:damage between 1.01 and 5%; 3: 5.01 and 25%, 4:25.01 and 50%, 5:50.1 and 75%, 6:75.01 and 100%. Herbivory subtotals were then calculated by multiplying the midpoint value of the herbivory class by the proportion of total leaves that fell into that class. Additionally, an assessment of the type of herbivory (defoliating/leaf chewing, galling, leaf-mining, or other) was noted for classes greater than zero (Barrio et al. 2018).

To examine the potential relationship between temperature variation along the study gradient and herbivory damage, we calculated the average amount of total herbivory damage observed from 9 to 19 July across our sites. Additionally, we estimated the total amount of damaged foliar biomass ($g{\cdot}\ m^{-2}$) by multiplying the mean cumulative July herbivory by foliar biomass estimates at each site (see above). Then, using the modelled air temperatures from the Landsat surface temperature estimates (see “Site selection and air temperature modelling”) we tested for relationships between temperature variations and foliar biomass, average July cumulative herbivory, and total damaged foliar biomass for both species across sites using Generalized Linear Models (GLM). GLMs were performed using JMP Pro 14.0.0 (SAS Institute Inc., Cary, NC). For all response variables, diagnostic plots were assessed to decide on the proper distribution and link function for each model. For all GLMs, we used a normal distribution model, but link functions varied: identity link for foliar biomass as distribution appeared normal, logit link for cumulative herbivory damage due to proportional data skewing towards lower values, and log link for total damaged foliar biomass due to a log-skewed distribution.

Insect community surveys

To explore variations in invertebrate community assemblage and structure across the environmental gradient and growing season, we consulted previously collected terrestrial arthropod samples from July 2016 (9–11 July and 19–20 July). Invertebrates samples were collected at various locations along the thermal gradient, but not at the same study sites as the leaf collection in 2017. Two locations were sampled at warm sites and two were designated cold sites. Sampling events were conducted with a leaf blower modified to vacuum (Asmus et al. 2018a, b; Wolkovich 2010). The same approximate volume of 4 m^2 (standardized by shrub height) of vegetation was sampled for each species for two minutes at each sample location. Collected sample material from the modified leaf blower were placed in 70% ethanol and identified to the lowest taxonomic unit. Additionally, between 5 and 10 individuals from each taxonomic unit were dried and weighed for estimates of average biomass. Then we categorized identified taxa according to feeding strategy (i.e., gallers, defoliators, leaf miners, predator) (Bocher et al. 2015). We tested for differences in the relative abundance of arthropod taxa between shrub species (*B. nana* and *S. glauca*) using χ^2 statistical analysis.

Results

Leaf expansion, foliar N, and cumulative herbivory across the growing season and thermal gradient

The average air temperature of warm sites was 2.3 °C warmer than cold sites, with an average temperature from June 1 to July 27 (± standard error) of 9.7 (± 2.1) °C and 7.4 (± 1.8) °C respectively, with temperatures ranging from 1.7 to 13.1 °C at the coldest sites and 2.3 to 16.3 °C at the warmer sites. These differences were observed both from land surface temperatures from Landsat 8 (Fig. 1a) and ambient air temperature loggers (Fig. 1b). Modeled June air temperatures calculated from Landsat 8 Land Surface temperatures ranged from 8.9 to 14.7 °C (Fig. 1a).

Leaf expansion occurred most rapidly from 15 June to early July for both deciduous shrub species (Fig. 2a, b). Locally weighted scatterplot smoothing is shown to demonstrate general trends of data across the field season. This period of expansion coincided with the warmest air temperature from this study, from 25 to 27 June 2017 (Fig. 1b). Foliar N concentrations, especially for *S. glauca*, were highest in early June and at the cold sites (Fig. 2c, d), with gradually decreasing N concentrations through June and into early July at all sites. Additionally, for *S. glauca*, the warmest site experienced the most rapid decrease in foliar N concentrations starting in mid-June (Fig. 2d).

Observed foliar herbivory damage remained below 0.05% for both species until 27 June (Fig. 2e, f). Throughout July, cumulative herbivory damage increased on both shrub species along the gradient, with warmer sites experiencing more foliar damage (Fig. 2e, f). Averaged foliar damage observed from 9 to 19 July, differed markedly in cumulative herbivory damage between warm and cold sites for both shrub species (Table 1). Over this period, for *B. nana*, we observed a

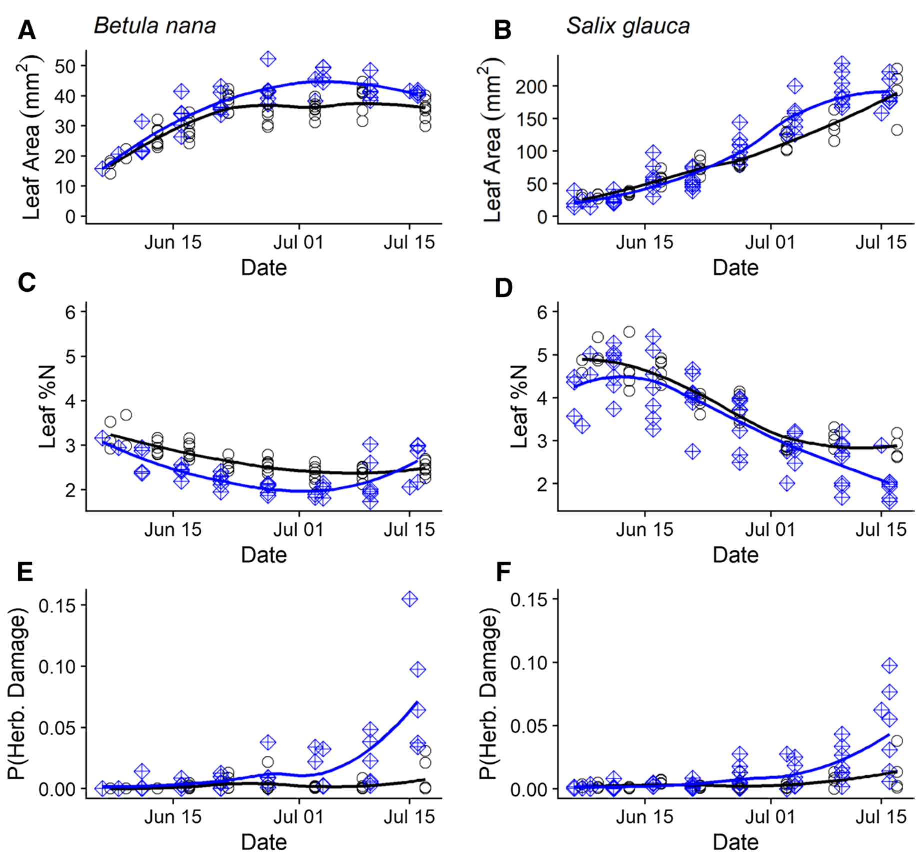

Fig. 2 Temporal trajectories of average leaf area (mm^2; **a**, **b**), leaf % foliar N on a per weight basis (**c**, **d**), and proportion of leaves with foliar herbivory damage (P(Herb. Damage) (**e**, **f**) from two deciduous Arctic shrubs, *Betula nana* (left column) and *S. glauca* (right column). Each point represented a plot-level average across the landscape gradient in West Greenland during the duration of the study in 2017. Circles designate cold sites and diamonds are warm sites (*n* = for each). Locally weighted scatterplot smoothing is shown to demonstrate general trends of data

Table 1 Summary of insect herbivory damage on measured leaves from 16 number of sites collected along a landscape gradient in West Greenland

Species	Temp. zone	Leaves	External damage	Mine damage	Gall damage	Total damage	Average leaf damage (%)
Betula nana	Cold	480	27	2	0	29	0.42
	Warm	482	88	0	0	88	4.14
Salix glauca	Cold	480	35	0	14	49	0.99
	Warm	470	84	8	27	119	3.21

Type of herbivory damage was recorded from leaves collected from 9–19 July 2017 across two temperature zones

mean foliar biomass loss and/or damage of 4.13% (ranging from 0.25 to 15.5%; Table 1) at warm sites, compared to just 0.42% foliar damage at cold sites (ranging from 0 to 3.1%; Table 1). We observed similar patterns in *S. glauca*, with warm sites experiencing an average of 3.21% damage to foliar tissue (ranging from 0.20 to 9.75%; Table 1), compared to 0.99% in cold sites (ranging from 0 to 3.78%; Table 1).

Foliar herbivory damage versus site temperature

There was a positive relationship between modeled gradient air temperatures and July average foliar herbivory damage for both *B. nana* and *S. glauca* (*Betula:* $\chi^2 = 8.5$, $df = 10$, $p = 0.003$; *Salix:* $\chi^2 = 6.6$, $df = 10$, $n = 12$, $p = 0.01$; Fig. 3c, d). Conversely, we found a negative relationship between air temperature and foliar biomass (g· m^{-2}) for both shrub

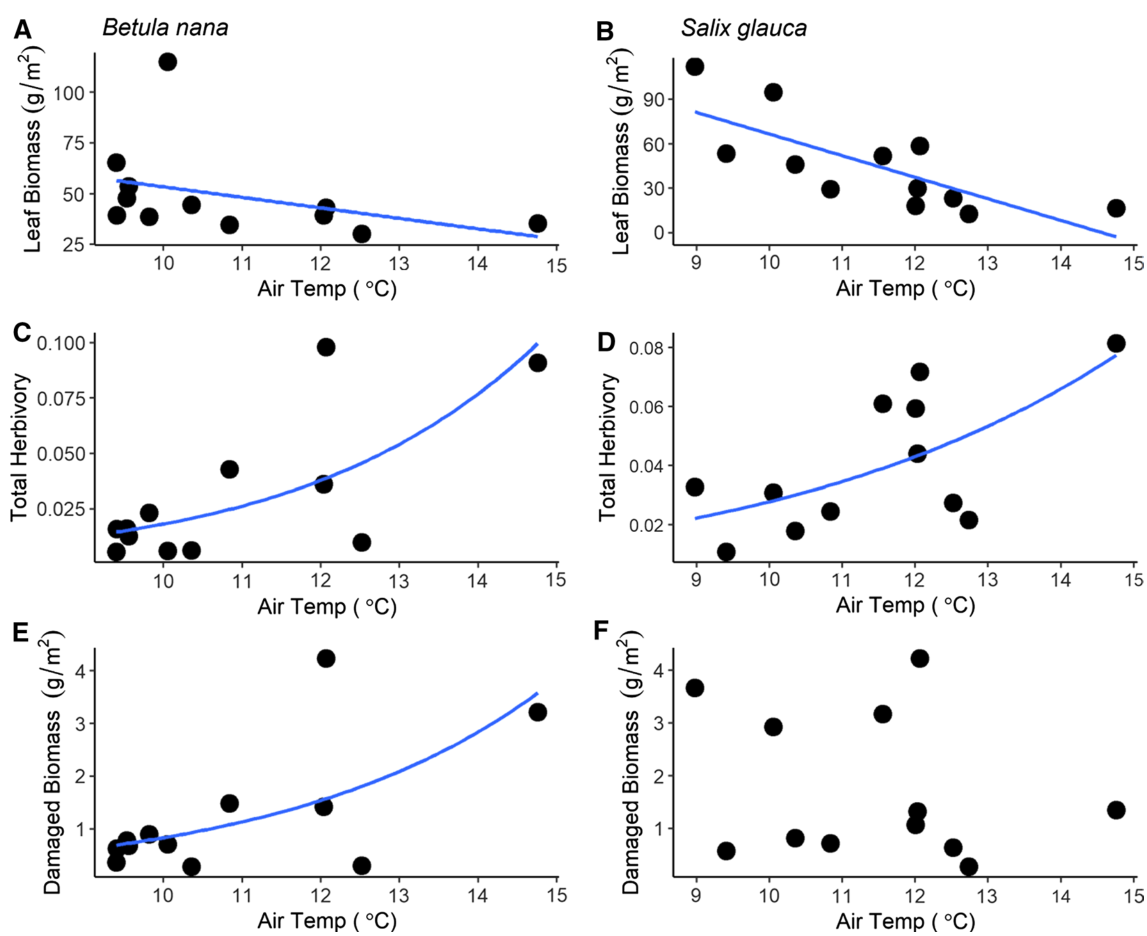

Fig. 3 General linear regression models of leaf biomass (g/m^2) (**a**, **b**), proportion of average July herbivory damage (**c**, **d**), and the total amount of foliage damaged by insect herbivores (g·m^{-2}) (**e**, **f**) from 9–19 July for *Betula nana* (left column) *and Salix glauca* (right column) versus modelled June air temperature from Landsat surface temperature estimates. Blue lines represent significant trends from generalized linear models (see text)

species (*Betula:* $\chi^2 = 4.5$, $df = 10$, $n = 12$, $p = 0.035$; *Salix:* $\chi^2 = 9.9$, $df = 10$, $n = 12$, $p = 0.001$; Fig. 3a, b). *S. glauca* shrubs experienced a steeper decline in foliar biomass with increasing temperature with a -14.6 ± 3.7 (SE) g· m^{-2} decrease versus a -3.3 ± 1.4 (SE) g m^{-2} decrease for *B. nana* shrubs. Total biomass damage removed by herbivores was positively related to temperature for *B. nana* but not for *S. glauca* (*Betula:* $\chi^2 = 6.1$, $df = 10$, $n = 12$, $p = 0.01$; *Salix:* $\chi^2 = 0.7$, $df = 10$, $n = 12$, $p = 0.39$; Fig. 3e,f).

Types of herbivory damage

From 9 to 19 July we assessed approximately 960 leaves of each species for herbivory damage and found that most of the observed damage was caused by defoliators (Table 1). Two times more observed herbivory damage occurred in warm vs cold sites for both shrub species (Table 1). In addition to defoliator damage, we observed leaf galls on *S. glauca*, which accounted for approximately 23% of the total observed herbivory in both warm and cold sites (Table 1). We also observed a small amount of leaf-mining in both *B. nana* and *S. glauca* (Table 1).

Arthropod vacuum surveys collected several different categories of potential herbivorous arthropods including seed-eaters, leaf miners, phloem feeders, defoliators, and gallers (Table 2). *B. nana* and *S. glauca* differed slightly with collected arthropod communities, with *B. nana* samples containing more Hemipteran species, while *S. glauca* samples contained more Acariformes. For both shrub communities, the most dominant herbivorous arthropod family was Hemiptera (Table 2). The seed-eating *Nysius groelandicus*, was found predominantly on *B. nana* while psyllids were commonly found on willows. Defoliators comprised several Lepidoptera, primarily larva of geometrid and noctuid moths. Other abundant herbivorous arthropods were and leafhoppers, which were found among both species of shrub. Dipteran leaf miners (Agromyzidae) were relatively sparse but were more abundant on *Salix* than *Betula*. We also identified a few mites (Acariformes) mostly on *S. glauca.* which we classified as gallers, Since mites occupy a wide array of feeding groups and we are unsure which of these mites were gall-forming we urge caution with interpreting these results.

Observed arthropod biomass differed between plant species at warm and cold sites (*Betula*·temp: $\chi^2 = 93.5$, $df = 15$, $n = 17$, $p < 0.001$, *Salix*·temp: $\chi^2 = 255.7$, $df = 15$, $n = 17$, $p < 0.001$). Notably, this included more Acariformes (mites) found in *S. glauca*, and within *Salix* there were more mites in cold sites than warm sites (Table 2). We observed more leaf-mining Diptera among warmer *Betula* shrubs (Table 2), although we did not observe any leaf mining in these sites (Table 1). Conversely, we found more Hemipteras from *Betula* shrubs at cold sites (Table 2).

Discussion

Insect herbivory across the growing season

Contrary to our initial prediction that arthropod herbivory would be more intense in the early part of the growing season, the majority of insect herbivory damage occurred in July, with little to no herbivory observed until around 27 June (Fig. 2). This differs from several other well-studied plant–herbivore systems, where expanding, nutrient-rich (higher foliar %N) leaves are more susceptible to herbivory (Aide 1993; Ayres and MacLean 1987; Coley 1983). Young leaf herbivory is often particularly pronounced in the tropics (Aide 1993; Coley 1983), where more plant biomass is regularly consumed by arthropod herbivores, compared to temperate and Arctic systems (sensu Latitude Herbivory Hypothesis; Coley and Barone 1996; Schemske et al. 2009). However, early-season herbivory is also observed to be important for arthropod development in some sub-Arctic communities (Ayres and MacLean, 1987; Ayres 1993; Dewar and Watt 1992), thereby bringing into question the importance of leaf expansion and phenology in northern plant–herbivore systems (Sweet et al. 2015; Diepstraten et al. 2018). A possible explanation for the lack of observed early-season herbivory in our study systems is that cold winter and spring temperatures likely impede arthropod development and emergence, allowing deciduous shrub leaves to

Table 2 Estimated biomass of herbivorous arthropods in g (mean ± SE), divided by taxon and feeding type from 9 to 20 July 2016

Shrub	Temp	Taxa (feeding type)				
		Acari (G)	Diptera (LM)	Hemi. (S, EF P)	Lepid. (EF)	Thysan. (P)
B. nana	Cold	2.1 (1.1) g	0.5 (0.1) g	35.9 (10.9) g	15.1 (3.3) g	0 g
	Warm	0.7 (0.2) g	3.9 (2.7) g	21.4 (9.6) g	4.1 (1.5) g	0.2 (0.2) g
S. glauca	Cold	7.4 (3.2) g	0.6 (0.2) g	27.0 (8.1) g	6.9 (0.8) g	0.6 (0.1) g
	Warm	3.2 (2.4) g	1.5 (1.4) g	70 (31.5) g	11.0 (3.3) g	0.4 (0.2) g

Four sites were sampled, two from cold areas and two from warm areas, for *Betula nana* and *Salix glauca.* Feeding types are abbreviated: *G* gallers, *LM* leaf miners, *S* seed eaters, *EF* defoliators, *P* phloem feeders

Taxa include Acari, Diptera, Hemiptera (Hemi.), Lepidoptera (Lepid.), and Thysanoptera (Thysan.)

develop with minimal herbivory (Coley and Barone 1996; Gao et al. 2019; Torp et al. 2010a, b). Additionally, climate change could be increasing asynchrony between the timing of bud burst and leaf emergence and the emergence of their respective invertebrate herbivores (Ayres 1993; Dewar and Watt 1992; Dixon 2003; Kharouba et al. 2018). For instance, insect emergence and development is likely governed by temperature (Ayres and MacLean 1987) while arctic shrub leaf emergence might be less variable intra-annually and better predicted by day of year and photoperiod (Post et al. 2016). Another possibility is that the West Greenland herbivorous arthropod community primarily feeds on mature vegetation, making the timing of bud burst less relevant for invertebrate herbivore growth and survival and overall rates of foliar damage. Finally, we cannot rule out that our methods and results did not fully capture deleterious effects of early-season herbivory as our study did not track herbivore damage that completely removed leaves or caused leaves to drop from the stem (Anstett et al. 2016).

Noticeable herbivory damage was largely caused by defoliators, presumably Lepidoptera and some Hemiptera (psyllids *Cacopyslla*) (Hodkinson and Bird 1998). Lepidoptera larva has the potential to cause the greatest damage to Arctic shrub leaves (Ayres and MacLean 1987; Barrio et al. 2016; Post and Pedersen 2008; Prendin et al. 2019), yet we found a decrease in the average count of Lepidoptera with temperature for *B. nana* and little to no difference with temperature for *S. glauca*. We, therefore, do not believe that increasing herbivory damage with temperature is caused by increasing arthropod numbers but instead caused by changes to arthropod physiology and behavior. Warming temperatures are known to increase arthropod metabolic demand (Ayres 1993; Rosenblatt and Schmitz 2016), whereby individuals may be consuming more biomass to meet nutritional requirements of rapid growth at warm versus cold sites (Ayres and MacLean 1987; Barrio et al. 2016; Torp et al. 2010a, b). Using feeding trials and a natural thermal gradient study design, Barrio et al. (2016) found that *Salix arctica* leaves experienced a greater intensity of herbivory and leaf loss due to caterpillars at warmer sites, coupled with a corresponding increase in measured caterpillar respiration. This suggests that increasing temperatures are likely directly impacting arthropod physiology and could be a key driver of our observed increases in foliar damage.

Consequences of herbivory for different shrub species

In addition to altering arthropod physiology, warming trends are influencing plant physiology via changes to environmental and edaphic conditions (Finger Higgens et al. 2020). Previous work along the same temperature gradient in west Greenland found that warmer air temperatures are highly correlated with increasing soil temperatures, drier soil conditions, and less available nitrogen, providing evidence of water and nutrient limitations on shrub growth (Finger Higgens et al. 2020; Gamm et al. 2017). Variations in soil water and nutrient availability can influence leaf quantity and quality, with ascending impacts on herbivores that are foraging to meet nutritional demands (Rosenblatt and Schmitz 2016). However, it should also be noted that beyond just temperatures, the gradient used in this study also captured an elevation gradient, with increasing winds and harsher climate conditions closer to the ice sheet (Heindel et al. 2015). Therefore, in addition to warming, it is possible that wind also contributed to variations in shrub structure (Finger Higgens et al. 2020).

In this study, shrubs in warmer, lower elevation environments had less foliar biomass than shrubs in cold sites (Fig. 3). Observed decreases in foliar biomass could lead to increases in observed foliar herbivory pressure. If foliar food resources become limiting due to plant water interactions, a stable population of would-be folivores would need to consume more of the remaining leaves to achieve nutritional demands. For example, in *S. glauca* a greater proportion of leaves with herbivory damaged did not translate to more biomass removed by herbivores. In fact, the amount of total biomass removed or damaged by invertebrate herbivores of *S. glauca* had no relationship with temperature and damage only increased with temperature for *B. nana*. Conversely, the observed increase in foliar damage with temperature for *B. nana* indicates that invertebrate herbivory could become a larger top–down control in warmer Arctic scenarios. (Rosenblatt and Schmitz 2016). Increasing temperatures are also suggested to reduce the production of anti-herbivory compounds in Arctic birch species (Graglial et al. 2001; Stark et al. 2015), thereby making birch leaves more palatable at warmer sites (Bryant et al. 2014). This divergence in total foliar biomass damage with increasing temperatures indicates that individual species sensitivities to shifts in plant–herbivore systems may differ with ongoing warming.

Because we observed differences in shrub foliar damage and temperature between our two shrub species, it is worth evaluating what warming might mean for the future compositions of Arctic vegetation communities. *Salix* shrubs could gain a competitive advantage if warming conditions result in less absolute leaf damage on *S. glauca* than *B. nana*. Additionally, the tundra of Greenland is prone to episodic outbreaks of caterpillar larva of *Eurosis occulta* (Post and Pedersen 2008; Lund et al. 2017; Prendin et al. 2019), which can have lasting, yet potentially different, impacts of shrub growth depending on the plant species (Post and Pedersen 2008). Dendrochronological work in Greenland suggests that *S. glauca* might be better adapted than *B. nana* to cope with and recover from severe defoliation events caused by caterpillar outbreaks (Gamm et al. 2017; Prendin et al. 2019). The replacement of shorter *B. nana* with taller *S. glauca* could also lead to changes in microclimate, with consequences for snow-capture (Sturm et al. 2001), arthropod communities (Asmus et al. 2018a, b), and decomposition and carbon cycling (Bjorkman et al. 2018). Therefore, the differences in species' responses to warming and herbivory are important to consider when forecasting the future of Arctic shrub communities.

Top–down controls on shrubification in a changing Arctic?

Early into the twenty-first century scientists began to note that Arctic shrubs were increasing across many Arctic tundra regions (Sturm et al. 2000; Myers-Smith et al. 2011), yet that steady increase of greenery has tempered within the last decade (Phoenix and Bjerke 2016; Epstein et al. 2017). There are a number of proposed limitations to shrub growth despite warmer temperatures and longer growing seasons, and herbivory can be a key top–down regulator of vegetation in the Arctic (Post and Pedersen 2008; Christie et al. 2015). However, most of the past work on shrub-herbivory has focused on vertebrate herbivory, drawing into question the importance of invertebrate herbivory in Arctic systems. Our findings, in conjunction with other collaborative projects through the Herbivory Network (https://herbivory.lbhi.is/; Barrio et al. 2018; Rheubottom et al. 2019), suggest that arthropod herbivory might broadly increase as temperatures continue to rise, potentially increasing stress on expanding vegetation. Additionally, as we suggest here, warming Arctic temperatures might lead to increases in arthropod metabolic demand and shifts in behavior which could potentially increase background herbivory despite stable invertebrate communities. While background herbivory remains low, ranging between 0.42 and 4.14% foliar damage in mid-July, small increases could be enough to limit gains in Arctic shrub growth. Continued work is needed to explore whether invertebrate damage to foliage is enough to stagnate shrub growth, by exploring arthropod, herbivore, and shrub leaf ecophysiology, and continued monitoring of Arctic plant–herbivore systems.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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