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## LETTER



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## Growth rings show limited evidence for ungulates' potential to suppress shrubs across the Arctic

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Supplementary material for this article is available [online](#)

## Abstract

Global warming has pronounced effects on tundra vegetation, and rising mean temperatures increase plant growth potential across the Arctic biome. Herbivores may counteract the warming impacts by reducing plant growth, but the strength of this effect may depend on prevailing regional climatic conditions. To study how ungulates interact with temperature to influence growth of tundra shrubs across the Arctic tundra biome, we assembled dendroecological data from 20 sites, comprising 1153 individual shrubs and 223 63 annual growth rings. Evidence for ungulates suppressing shrub radial growth was only observed at intermediate summer temperatures (6.5 °C–9 °C), and even at these temperatures the effect was not strong. Multiple factors, including forage preferences and landscape use by the ungulates, and favourable climatic conditions enabling effective compensatory growth of shrubs, may weaken the effects of ungulates on shrubs, possibly explaining the weakness of observed ungulate effects. Earlier local studies have shown that ungulates may counteract the impacts of warming on tundra shrub growth, but we demonstrate that ungulates' potential to suppress shrub radial growth is not always evident, and may be limited to certain climatic conditions.

## 1. Introduction

Tundra vegetation is known to be sensitive to climatic changes (Chapin *et al* 1992, Bjorkman *et al* 2020, Myers-Smith *et al* 2020). During the past decades, the warming Arctic has experienced increases in vegetation cover, height, biomass and abundance, resulting in greening (Carlson *et al* 2017, Bjorkman *et al* 2018, Bolton *et al* 2018, Bjorkman *et al* 2020, Berner *et al* 2020, Buchwal *et al* 2020). Along this continuing transition, changes in species composition (Niskanen *et al* 2017, Boscutti *et al* 2018), phenology (May *et al* 2017, Prev y *et al* 2019), and ecosystem functioning (Leffler *et al* 2016, Yu *et al* 2017, Jespersen *et al* 2018, Bret-Harte *et al* 2019) are expected and observed. In addition to threatening Arctic flora and fauna dependent on open habitats, increased shrub abundance (Naito and Cairns 2011, Myers-Smith and Hik 2018, Vowles and Bj rk 2019, Garc a Criado *et al* 2020) may even change albedo and soil carbon storage, with feedbacks to climate (Sturm *et al* 2005, Bonfils *et al* 2012, Cahoon *et al* 2012b, DeFranco *et al* 2020). However, recent studies have shown that tundra vegetation changes are anything but uniform (Berner *et al* 2020, Bjorkman *et al* 2020, Myers-Smith *et al* 2020), suggesting that factors other than abiotic conditions also play a role in shrub growth and abundance.

The circumpolar tundra is characterized by strong interactions between herbivores and plants (Oksanen *et al* 2020), and a key role in these interactions is played by ungulates. Shrubs have been shown to be affected by foraging and/or trampling by all

large tundra ungulates, including reindeer/caribou (*Rangifer tarandus*; Olofsson *et al* 2004, 2009, Cahoon *et al* 2012a, Cohen *et al* 2013, Plante *et al* 2014, Kaarlej rvi *et al* 2015, Vowles *et al* 2017, Yl nne *et al* 2018), muskoxen (*Ovibos moschatus*; Post and Pedersen 2008, Mosbacher *et al* 2019) and sheep (*Ovis aries*; Speed *et al* 2013, Ross *et al* 2016). Ungulate effects can match climate effects by slowing down, stopping or even reversing increases in woody plant growth, biomass and cover caused by warming, and thus they have been suggested to be able to function as a buffer of the effects of climate warming: to conserve the tundra as an open habitat, retain its ecosystem functions and even increase its albedo, slowing down the climatic warming (Olofsson *et al* 2009, Cahoon *et al* 2012a, Speed *et al* 2013, Plante *et al* 2014, Christie *et al* 2015, Vowles *et al* 2017, Speed *et al* 2021). The potential of ungulates to control woody plant growth is strikingly demonstrated in northern Fennoscandia, where ungulates appear to have stabilized tree lines (Aune *et al* 2011, Vuorinen *et al* 2017) and suppressed shrubs (den Herder *et al* 2008, Pajunen *et al* 2012, Br then *et al* 2017), in spite of a warming climate.

It is, however, unclear whether and how this potential ungulate buffer varies across the tundra. For example, precipitation and moisture conditions may change shrubs' response both to ungulates and to warming (Buchwal *et al* 2020). Furthermore, different climatic regimes of the Arctic harbour different shrub and ungulate species, likely leading to different buffer strengths (Bryant *et al* 2014). Particularly, interactions between ungulates and climate remain understudied (Olofsson and Post 2018, Andruko *et al* 2020,

García Criado *et al* 2020). Climate and ungulates are rarely simultaneously quantified in studies of tundra ecosystems (Welker *et al* 2004, Plante *et al* 2014, Christie *et al* 2015, Vuorinen *et al* 2017), and the existing studies are usually undertaken at local scale with differing methods (Olofsson *et al* 2009, Speed *et al* 2013, Kaarlejärvi *et al* 2015), making it challenging to scale up effects to a pan-Arctic level. Thus, while it is clear that ungulates can, in principle, modify climate effects, we do not know under what conditions ungulates can effectively reduce the growth of shrubs across the Arctic.

During the past decades, the tundra biome has experienced simultaneous changes in climate (Box *et al* 2019, Bjorkman *et al* 2020, Myers-Smith *et al* 2020) and in herbivore densities (Vors and Boyce 2009, Speed *et al* 2019, Andruko *et al* 2020, Cuyler *et al* 2020), and the concurrent nature of these changes has made it hard to disentangle their effects on vegetation dynamics. In this study, we address this challenge by examining the radial growth of deciduous shrubs, woody plants that play a central part in tundra vegetation change by driving the vegetation structure, albedo, carbon balance and other key ecosystem properties (Naito and Cairns 2011, Myers-Smith and Hik 2018, Vowles and Björk 2019, García Criado *et al* 2020). The growth rings of these shrubs provide a standardized basis for assessment of radial growth variation over decades and large spatial scales (Myers-Smith *et al* 2015b), enabling analysis across the tundra biome (Buchwal *et al* 2020). We compiled shrub ring measurements from 20 sites (figure 1, appendix S1: table S1 available online at [stacks.iop.org/ERL/17/034013/mmedia](https://stacks.iop.org/ERL/17/034013/mmedia)) to quantify the effect sizes of summer temperature and ungulate densities on shrub growth under different conditions, and to answer the question: does the response of shrub radial growth to ungulates depend on summer temperature conditions across the Arctic? In addition, we relate the results to summer precipitation, winter precipitation, and ungulate and shrub species to identify whether these factors could be linked to the shrub growth patterns observed under different ungulate density and summer temperature conditions.

## 2. Data and methods

### 2.1. Shrub data

We assembled a database that comprised published and unpublished shrub ring width data from 20 sites across the arctic and oroarctic tundra (*sensu* Virtanen *et al* 2016; figure 1). The data came from three functionally distinct deciduous shrub groups: dwarf birch (*Betula nana*, *B. glandulosa*), two small, prostrate *Salix* species (*S. arctica*, *S. polaris*) and five large, erect *Salix* species (*S. pulchra*, *S. glauca*, *S. richardsonii*, *S. lapponum*, *S. lanata*). The chronologies that were long enough were cross-dated to other shrub individuals

at the same site, shorter ones only within each stem section (S); for details on this data, see appendix S1: table S1.

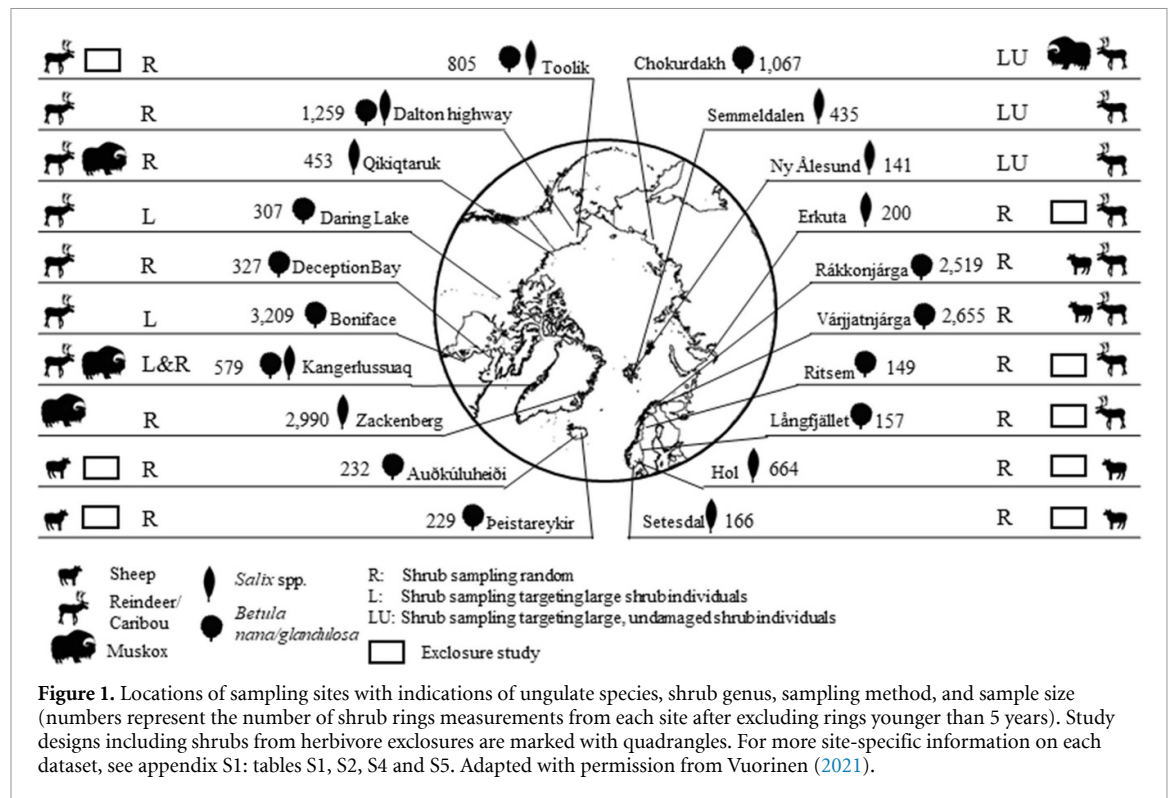
Ring widths were converted to approximation of basal area increment (BAI) by using the *dplr*-package (Bunn *et al* 2019) to account for geometrical growth trends, assuming that ring circumference can be approximated by a circle (Biondi and Qeadan 2008). While exact area increment measurements are more precise, it was not feasible to acquire them in our study given the number of samples and collation of data from multiple studies. To meet the assumption of normality, BAI was log-transformed prior to analyses.

The original data included 1388 individual shrubs and 269 71 ring measurements (figure 1; appendix S1: tables S1 and S2). Prior to the analysis, we excluded ring measurements of younger than 5 years of shrub age to account for typical irregular growth patterns of young individuals (Myers-Smith *et al* 2015a, 2015b). After applying this constraint, and excluding years with no ungulate data, we retained 223 63 ring measurements from 1153 shrubs, covering the time period of 1973–2018. Missing rings (*i.e.* years with no growth) were included in the analysis as zeros, as they may form as a response to browsing or unfavourable climatic conditions; the results were, however, not sensitive to their removal (table S3).

### 2.2. Ungulate data

We acquired ungulate density data on all ungulate species with body mass >50 kg occurring at the study sites, namely reindeer/caribou (*R. tarandus*), muskox (*O. moschatus*) and sheep (*O. aries*). We utilized multiple data sources, acquiring the best available density information for each site (the sources provided in the reference column in table S4). The size of the area over which ungulate densities were estimated differed between the sites, and therefore the values had some variation in spatial precision (for the areas over which ungulate densities were estimated, see the ‘area size(s)’ column in table S4).

In most cases, ungulate density data were available for each year (see the ‘covered years’ column in table S4). However, if data were missing for certain years but the population deemed to be relatively stable over these years, missing data were interpolated assuming a linear change (also specified in the ‘covered years’ column in table S4). After thus acquiring annual density data for each site for each year, we converted the density data to approximate metabolic biomass per square kilometre per year (*i.e.* biomass<sup>0.75</sup>, kg km<sup>-2</sup>). Data on body size variation within ungulate populations was not available in most cases, and thus we used average male weight to acquire the potential maximum metabolic biomass density. The weights used were 300 kg for muskox, 150 kg for reindeer/caribou (with the exception of Yamal and Svalbard reindeer that are known to be smaller; 127



and 90 kg, respectively), 85 kg for Norwegian sheep and 65 kg for Icelandic sheep (Olesen *et al* 1994, Ross *et al* 2016). We expect this approach to capture reasonable interannual variation and approximate site differences in unguulate density. Annual biomass values were log-transformed before analyses to homogenize the residual variance.

In addition to the observational unguulate values, experimental unguulate enclosures provided conditions with zero herbivore pressure (see the ‘enclosures’ column in table S4).

### 2.3. Climate data

We used climate data from the Climatic Research Unit Time-Series version (CRU TS 4.03) of high-resolution gridded data of month-by-month variation in climate (CRU TS 4.03; Harris and Jones 2019), a global climate model on a 0.5° latitude by 0.5° longitude grid that covers the time period of 1901–2018 and thus all our shrub chronologies (appendix S1: table S1). This data correlates highly with climate data from meteorological stations across the Arctic tundra (Myers-Smith *et al* 2015a). For each of the shrub sampling sites, we extracted monthly mean temperature and precipitation data covering the available shrub growth chronology periods. The repeated site mean values that are used to gap fill CRU data (Macias-Fauria *et al* 2014) were removed. For data from Svalbard and the Dalton Highway (figure 1), this resulted in considerable drop in available precipitation data (values

not available for >30% of shrub chronology data points), and thus we substituted CRU data with local climate station data in these two cases (appendix S1: supplementary methods 1). Annual averages for mean summer temperature (June–August), summer precipitation (June–August) and winter precipitation (October–April) were then calculated for each shrub sampling site. As precipitation does not necessarily describe the local soil moisture conditions, each data contributor was asked to assess the moisture class of the site based on three classes: (a) dry: soil is dry to the touch throughout the summer, apart from just after rain; (b) moist: soil is wet to the touch throughout most of the summer apart from particularly dry spells; (c) wet: standing water is present and the soil is saturated throughout the summer (Myers-Smith *et al* 2015a). All sites were described as either dry or moist on average, i.e. there were no wet sites in our network.

### 2.4. Statistical analyses

To be able to test for unguulate interactions reliably, data needed to be balanced across the captured unguulate density range. To achieve this, we ran two separate analyses: (a) to test the effects of variation in observational unguulate density, and (b) to test the effects of experimental presence-absence of unguulates. In the first analysis, we included only the data points outside of the experimental enclosures. In the second analysis, we only included data from within enclosures and from corresponding open control areas including

only shrub rings grown after the enclosure fence installation. The observed ungulate density analysis included 183 27 BAI values from 1078 shrub individuals from 20 sites (see appendix S1: figure S1 for distribution of data in time, and shrub ages). As the number of ungulate exclusion studies was limited and exclusion times typically short, the experimental ungulate exclusion analysis only included 2936 BAI values from 247 shrub individuals from eight sites (appendix S1: table S5).

In the observed ungulate density analysis, we modelled log-transformed BAI as a response to annual ungulate metabolic biomass density, summer temperature, summer precipitation, winter precipitation and interaction of summer temperature and annual ungulate metabolic biomass density in a linear mixed-effects model, by using lme-function of the nlme-package (Pinheiro *et al* 2017). Shrub age was used as a log-transformed covariate as we found a non-linear relationship between age and BAI (appendix S1: figure S2). We also fitted a quadratic term for summer temperature, as we expected that the shrub growth response to temperature may turn negative at high temperatures, especially if warm summer conditions are associated with longer snowy period or drying events in spring (Phoenix and Bjerke 2016). Values of summer temperature, summer precipitation and ungulate density were values from the same shrub growth year, whereas values of winter precipitation were from the previous winter (i.e. including winter months of the previous year). Spatial and temporal dependencies were accounted for by nesting shrub individuals within sites and sites within years as random factors in both analyses. Variance inflation factor (VIF)-values of linear effects were checked for potential collinearity issues, and remained acceptable (table 1; Graham 2003). Soil moisture classification was not included as a fixed effect into the model as its primary purpose was to ensure that soil moisture was not collinear with other environmental variables (appendix S1: figure S3(c)). We also did not include shrub or ungulate species as fixed effects into the model as we knew that these variables would necessarily be collinear with summer temperature; the potential underlying effects of ungulate and shrub species are discussed in the section 3. Potential time-lagged effects of ungulates and climatic factors were tested with equivalent models where BAI was explained by ungulate density and climatic factors from 1, 2 and 3 years before the shrub growth took place (table S6).

The experimental ungulate exclusion analysis was similar to that of the analysis looking into the effects of observed ungulate density, but annual ungulate density was replaced with annual ungulate presence-absence. In addition, we had to exclude winter precipitation as it was collinear with summer

precipitation in this dataset, and thus these two variables could not be disentangled. Summer precipitation was selected as it was deemed to be more likely driver for shrub growth than winter precipitation.

As we had two continuous main variables (summer temperature and annual ungulate density) and a continuous response variable (BAI), we visualized this three-dimensional data by heat maps where  $y$ -axis represented annual ungulate density,  $x$ -axis represented summer temperature, and the predicted BAI-values were presented as colour on this summer temperature—ungulate density plain. This also allowed us to visualize potential interactive collinearities with other climatic variables that cannot be detected by VIFs.

All analyses were carried out within the R environment (R version 3.5.1, R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

### 3. Results

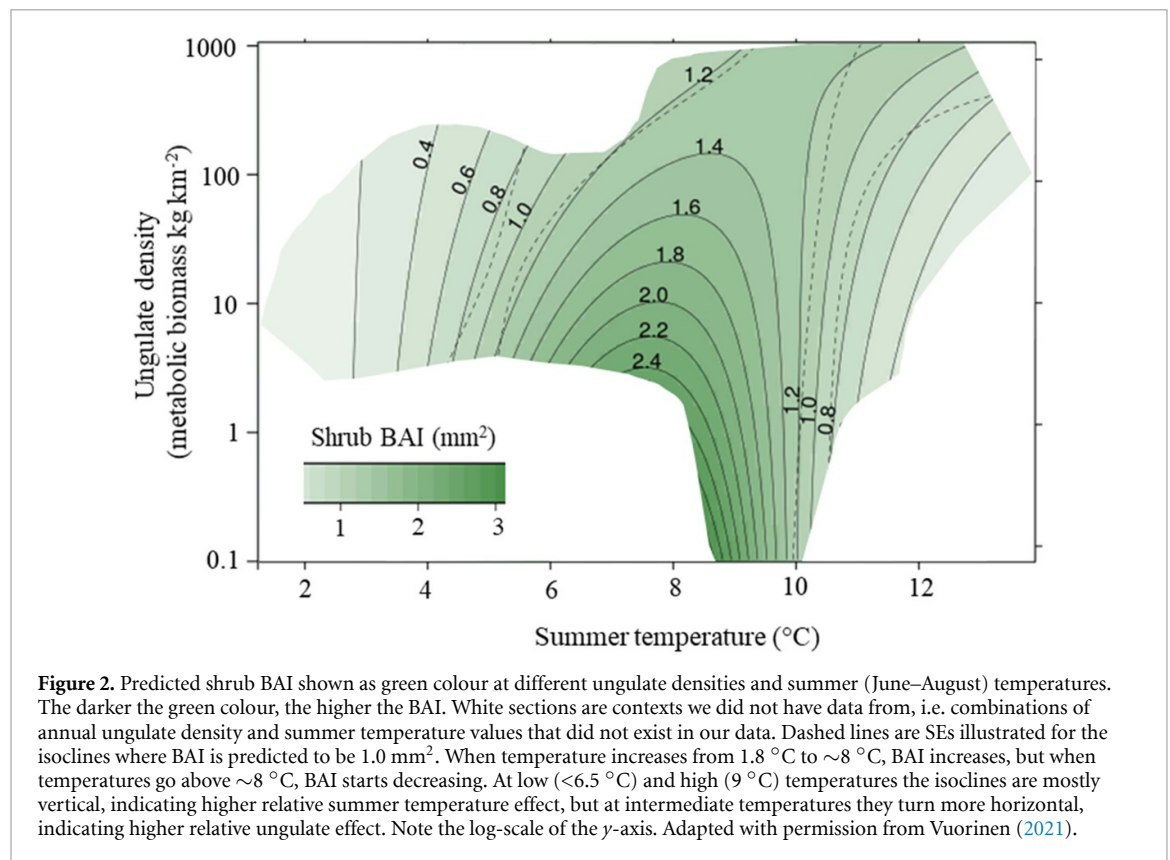
Most of the explained shrub radial growth variation was attributed to summer temperature, and to a lesser extent to shrub age and summer precipitation (table 1). The observed positive summer temperature response levelled off above  $\sim 8$  °C and turned slightly negative (table 1, appendix S1: figure S4). Summer temperatures lower than  $\sim 5$  °C were generally accompanied by low summer and winter precipitation, whereas at higher temperatures, we observed a wider range of precipitation values (appendix S1: figures S3(a) and (b)), but this collinearity is not expected to distort the temperature effect estimates (see VIF-values in table 1).

Annual ungulate density explained a negligible part of the observed variation in shrub radial growth (table 1). Furthermore, annual ungulate density interacted with summer temperature (table 1) in such a way that its effect was only detected at a narrow range of intermediate summer temperatures of 6.5 °C–9 °C, implying that ungulates had no detectable effect on shrub growth in most parts of the temperature gradient across the Arctic (figure 2). When the annual ungulate density effect was examined separately for the intermediate (6.5 °C–9 °C), low (<6.5 °C) and high (>9 °C) summer temperatures, its effect size appeared minor even at intermediate temperatures (figure 3). Time-lagged analyses supported this finding (appendix S1: table S6).

We did not find ungulate exclusion effects on shrub radial growth, neither as a main effect nor as an interaction with temperature (appendix S1: table S7), although this may have been due to low amount of data and short chronologies from the majority of the enclosure sites, reflecting the relatively short experimental ungulate exclusion periods ( $13 \pm 9$  years; appendix S1: table S5).

**Table 1.** Coefficients for the main model with annual ungulate metabolic biomass density: estimates, standardized estimates, standard errors, adjusted standard errors,  $t$ -values and Wald-test based  $p$ -values. Variance inflation factors (VIF-values) and partial  $R^2$ s ( $\pm$ CL) are given for the main effects. Variables with superscript 2 refer to quadratic effects. Marginal  $R^2$  of the model was 0.32, and  $df = 178$ . Partial  $R^2$ s were calculated by  $r2beta$ -functions in  $r2glmm$ -package. Adapted with permission from Vuorinen (2021).

	VIF	$R^2$	Est.	Std. Est.	Std. Err.	$t$	$p$
Intercept	—	—	8.26	14.31	0.411	20.1	<0.0001
Ungulate density	1.1	$0.1 \pm 0.1$	0.35	-0.23	0.254	1.4	0.1664
Summer temperature	1.1	$11 \pm 0.9$	1.13	0.03	0.107	10.6	<0.0001
Summer temperature <sup>2</sup>	—	$8.2 \pm 0.8$	-0.07	-0.60	0.007	-10.3	<0.0001
Ungulate density: summer temperature	—	$1.5 \pm 0.2$	-0.18	0.21	0.060	-3.0	0.0031
Ungulate density: summer temperature <sup>2</sup>	—	$2.5 \pm 0.2$	0.01	0.17	0.004	4.0	0.0001
Summer precipitation	1.6	$3.8 \pm 0.6$	0.54	0.39	0.073	7.4	<0.0001
Winter precipitation	1.5	$0.1 \pm 0.1$	0.04	0.05	0.031	1.2	0.24
Age	1.0	$5.6 \pm 0.7$	0.48	0.32	0.014	33.9	<0.0001

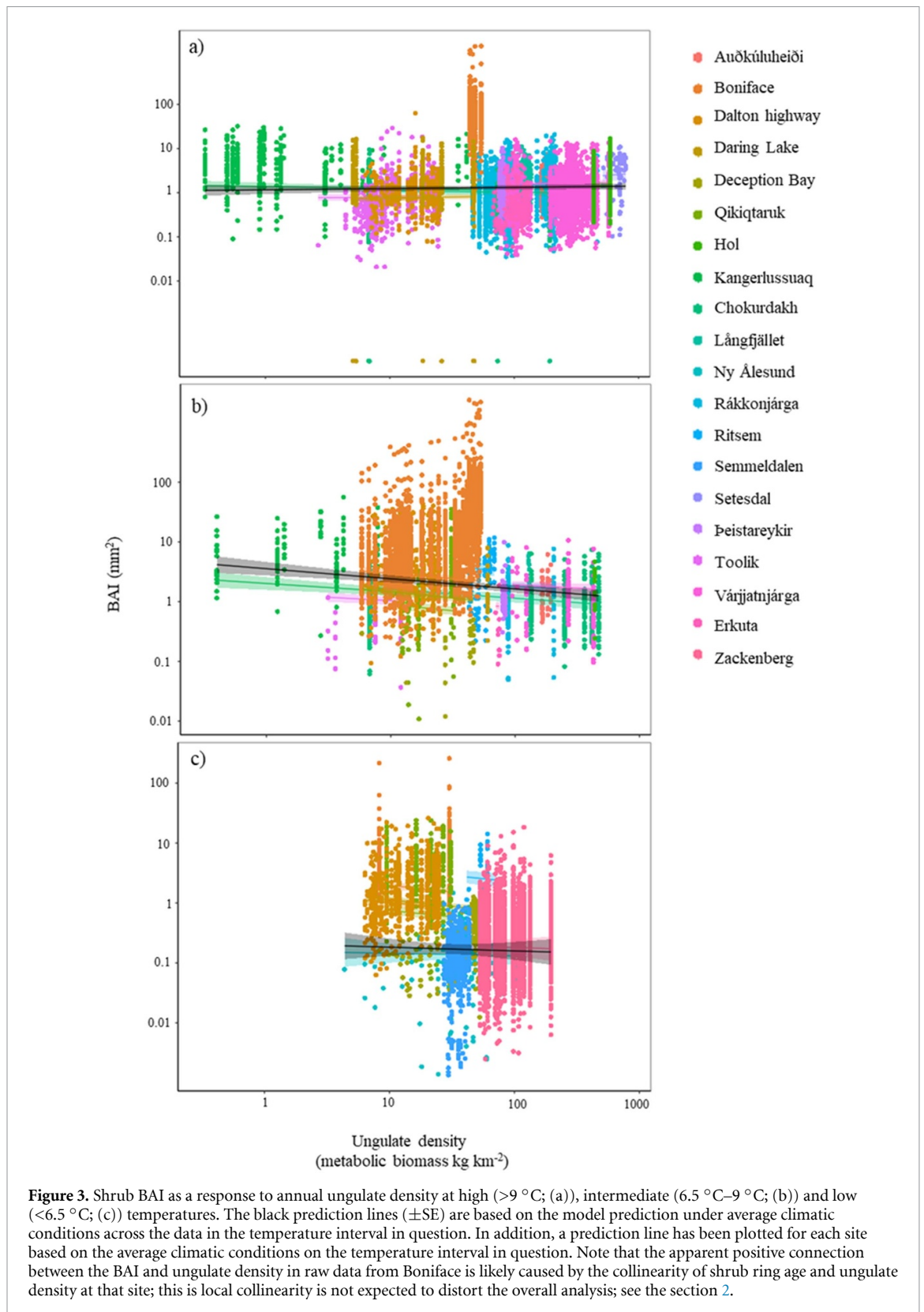


#### 4. Discussion

Our results corroborate the climate sensitivity of Arctic tundra shrub growth (Bjorkman *et al* 2020, Buchwal *et al* 2020, Myers-Smith *et al* 2020), but we found only limited evidence for ungulates' potential to inhibit shrub growth: shrub radial growth response to ungulates was weak and depended on summer temperature conditions across the different climatic regimes of the Arctic. It has been suggested that herbivores could be used to mitigate the effects of climatic changes in various ecosystems (Cromsigt *et al* 2018, Macias-Fauria *et al* 2020), and it is known that herbivores can inhibit plant growth on tundra (Post and Pedersen 2008, Olofsson *et al* 2009, Speed *et al* 2010, Christie *et al* 2015, Bråthen *et al* 2017,

Vowles *et al* 2017) and in boreal forests (Fisichelli *et al* 2012, Vuorinen *et al* 2020a, Vuorinen *et al* 2020b) under certain conditions. However, our results indicate that the potential of herbivores to buffer the effect of warming on tundra ecosystems should not be taken for granted.

The results suggest that climate itself may constrain herbivores' potential to suppress woody plants. If there is no water limitation, that typically occurs in for instance, moist tussock tundra (Jespersen *et al* 2018), shrubs may express efficient compensatory growth after browsing, leading to negligible ungulate effect (Champagne *et al* 2012). This could explain why we did not detect ungulate effects under high temperatures (>9 °C) where high precipitation values were associated with high ungulate densities



(appendix S1: figure S3(a)). At high temperatures, high ungulate densities also occurred in the areas with high winter precipitation (appendix S1: figure S3(b)) and hence where snow cover could protect shrubs from ungulate herbivory. Furthermore, snow provides an important water source in the subsequent summers enhancing C gain, especially

late in the summer when summer-droughts may be prevalent (Jespersen *et al* 2018). Deeper snow can also accelerate winter-long nitrogen mineralization providing additional nutrients, further enhancing shrub growth (Schimel *et al* 2004, Welker *et al* 2005). If climatic and soil conditions enable compensatory growth or prevent ungulates' access to shrubs,



ungulate effects may be considerably weakened. It is also possible that when abiotic growth conditions are optimal (as they appear to be under intermediate temperatures), ungulate effect can be seen due to lack of other constraints, whereas under more extreme abiotic growth conditions, ungulate effects are overridden by temperature and moisture availability constraints.

Rather than climate *per se*, ungulate effects may also be limited by biotic factors that differ between climatic regimes. Perhaps the most crucial one of such confounding factors is ungulate behaviour. The way ungulate individuals are dispersed in space and time (Schmidt *et al* 2016, Skarin *et al* 2020, Pedersen *et al* 2021) modifies the effect of ungulate density, and the shorter time they are present at a site during the year, the weaker their effect is likely to be. For example, the Riviere-aux-Feuilles caribou herd, included in our data, migrates through the easternmost shrub sampling site in the Canadian Arctic once a year (Nicholson *et al* 2016, Morrissette-Boileau *et al* 2018), whereas colder, northern summer grazing sites are exposed to more constant ungulate pressure (figure 1). Even when present at a site, ungulates may not use all parts of the landscape, meaning that they do not trample or forage vegetation evenly, possibly leaving a considerable fraction of the shrubs intact. It should also be noted that changes in snow may have considerable effects on ungulate movements; especially as how the synoptic climatology in autumn and the way winter comes to the Arctic appears to affect the depth and distribution of snow and the distribution and foraging behaviour of caribou (Pedersen *et al* 2021).

Interestingly, under temperatures where we observed ungulate populations that were mostly sedentary, such as reindeer in Svalbard and sheep across Scandinavia (Speed *et al* 2014; appendix S1: figures S5(a) and S6), ungulate effects were mostly absent. This might be explained by another aspect of ungulate behaviour, namely, foraging preferences (Welker *et al* 2005, Richert *et al* 2021). If the landscape has plant species with higher palatability, such as graminoids and forbs, ungulates may not target shrubs, and thus have no effects on their growth. In our data, sites with high summer temperature, high precipitation, and high ungulate density were typically dominated by sheep (appendix S1: figure S5(a)) that, as grazers (Hofmann 1989, Kausrud *et al* 2006) favouring other plants over shrubs, may not be efficient in inhibiting shrub growth. This may contribute to the lack of ungulate effects under high summer temperatures. For the conditions typical for mild, moist, sheep-dominated southern Norway, the model even predicted a moderate positive ungulate density effect (shown by isoclines inclined to the left at temperatures above  $\sim 10$  °C and at ungulate densities above  $\sim 100$  kg km<sup>-2</sup> in figure 2; these are the conditions typical for sites in southern Norway,

as shown in appendix S1: figure S6). This is possibly driven by suppression of competing plants by sheep (Speed *et al* 2013, Bråthen and Lortie 2016). At the coldest sites in our data, located in Svalbard and Greenland (appendix S1: figure S6), sedentary reindeer and muskox (Schmidt *et al* 2016, Beumer *et al* 2020), may similarly prefer graminoids and forbs, possibly contributing to the lack of ungulate effect in the High Arctic.

Along the biotic characteristics of ungulates, browsing and trampling effects can be modified by the biotic characteristics of shrubs. The species sampled in the High Arctic were small and prostrate (table S1), and thus not necessarily damaged by ungulates to the same extent as taller, erect shrub species typical for lower altitudes and latitudes (Vowles and Björk 2019). This may contribute to the lack of ungulate effect in the High Arctic. It can also be questioned whether the observed ungulate density and summer temperature effects were simply indirect effects resulting from shrub species changes in space along the ungulate density and summer temperature gradients: at cold temperatures, only prostrate *Salix* species were present, whereas at higher temperatures, the shrub species pool consisted of tall *Salix* species and *B. nana/glandulosa* (appendix S1: figures S4(c), S5(b) and table S1). However, the most prevalent genus, *Betula*, showed the above-described patterns when analysed separately from other shrubs (appendix S1: figure S7), indicating that the observed general patterns cannot be accounted solely to spatial differences between shrub species. Yet, it is apparent that when evaluating ungulates' potential to inhibit shrub growth, ungulate selectivity and shrub sensitivity should be accounted for (Bryant *et al* 2014). For example, it has been suggested that browsing is likely to slow birch expansion in Fennoscandia and western Siberia as these areas are dominated by less effectively defended non-resin birches, whereas in the North-American mainland, browsing is less likely to slow birch expansion as the prevailing birch species are more effectively defended through resins (Bryant *et al* 2014, Richert *et al* 2021).

Considering all constraints that may limit ungulates' potential to suppress plants, from climatic factors to ungulate behaviour and shrub characteristics, we conclude that herbivores' potential to suppress shrubs are likely to remain negligible under current conditions. While vertebrate herbivore communities may also change with climatic warming, this is more likely to be driven directly by temperature, rather than through vegetation change (Speed *et al* 2021). When assessing ungulates' potential to counteract climatic effects, it is also crucial to examine the importance of the ungulate effect in relation to other factors shaping plant growth, such as soil nutrients, microclimate and tundra type (Epstein *et al* 2008), that may contribute to shrub growth variation more than landscape-scale ungulate densities

and mean temperatures incorporated in this study, as well as mediate ungulate and temperature effects. It is also known that, for example, rodents and insect outbreaks can modify shrub growth, potentially exceeding the effect sizes of ungulate herbivores (Post and Pedersen 2008, Ravolainen *et al* 2014, see also Vowles *et al* 2016, Prendin *et al* 2020).

It is also crucial to note that ungulates' potential to suppress shrubs depends on the ungulate density. Even though we only observed constrained evidence for ungulates' potential to suppress shrub growth, it can be expected that ungulate densities higher than observed here can have more drastic effects on shrub growth. Particularly in the High Arctic, we might have failed to identify ungulate effects because there our data captured less variation in ungulate densities compared to the warmer regions (figures 2 and 3). It is also possible that even though ungulates may not be able to effectively suppress shrub radial growth across the Arctic, they may induce changes e.g. in shrub mortality and height, suppressing shrubification.

Our results indicate that shrubs might not benefit from warming in a linear manner. This observation is in line with earlier studies showing stability and even browning trends in tundra vegetation under warming climate (Phoenix and Bjerke 2016, Myers-Smith *et al* 2020). Increasing temperatures may eventually lead to constant or even decreasing shrub growth due to non-linear growth responses to temperature (appendix S1: figure S4), moisture limitations (Naito and Cairns 2011, Myers-Smith *et al* 2015a, Ackerman *et al* 2017, Buchwal *et al* 2020) and extreme climatic events associated with high average summer temperatures, such as drought events, spring stress (Welker *et al* 1993, 2005, Gamm *et al* 2018), and icing events related to winter precipitation (Le Moullec *et al* 2020; figure S3(b)). This implies that the ability of herbivores to buffer climatic impacts may even become irrelevant under a warmer climate. Further studies are needed to assess how non-linear climatic responses of plants relate to herbivore responses, and how they might be affected by differences in biotic characteristics of different plant and herbivore species. Our results pertain to the radial growth of mature shrub stems, but ungulate effects on shrub height growth or horizontal spread via sexual or vegetative reproduction might differ from those presented here, and thus it is also crucial to conduct large-scale studies on other shrub characters than radial growth, such as shrub cover, height and stem establishment rate (Myers-Smith *et al* 2015b), to understand how climate and herbivores interact in shaping shrubification trends.

### Data availability statements

Climatic Research Unit Time-Series version 4.03 of high-resolution gridded data of month-by-month variation in climate (CRU TS 4.03; Harris and

Jones 2019) is available at CRU repository ([https://crudata.uea.ac.uk/cru/data/hrg/cru\\_ts\\_4.03/](https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.03/); see also <https://catalogue.ceda.ac.uk/uuid/10d3e3640f004c578403419aac167d82>). Ungulate data sources are given in appendix S1: table S4.

Shrub datasets (as specified in appendix S1: table S1) are available at following repositories:

Chronologies from Dalton Highway, Toolik, Deception Bay, Zackenberg, Audkuluheidi, Theistareykir, Ritsem, Långfjället, Setesdal, Hol (Speed *et al* 2013), Rakkonjarga, Varjjatnjarga, Erkuta and Chokurdakh (Li *et al* 2016) on Dryad.

Chronologies from Semmeldalen and Ny-Ålesund (Le Moullec *et al* 2019, Le Moullec *et al* 2020) on Dryad (<http://dx.doi.org/10.5061/dryad.k3j9kd54c>, and <http://datadryad.org/resource/doi:10.5061/dryad.d7p3b40>).

Chronologies from Kangerlussuaq on the NSF Arctic Data Center (<https://arcticdata.io/catalog/#view/urn:uuid:3dc91064-7b8b-4308-b949-a361b7146baa>).

Chronologies from Boniface (Ropars 2015) on Dryad (DOI: 10.5061/dryad.n812k).

Chronologies from Daring lake (Andruko *et al* 2020) on the Polar Data Catalogue (<http://link.springer.com/article/10.1007/s10021-019-00474-7>).

Chronologies from Qikiqtaruk on GitHub repository for the ShrubHub growth ring database (<https://github.com/ShrubHub/ShrubringHub>; Myers-Smith *et al* 2015a) and on Qikiqtaruk Ecological Monitoring Database (DOI: 10.5281/zenodo.2397996; <https://zenodo.org/record/2397996#.X2scO2gzZaQ>).

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