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To cite this article: Katariina E M Vuorinen *et al* 2022 *Environ. Res. Lett.* **17** 034013

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ENVIRONMENTAL RESEARCH
LETTERS

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

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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, Prevéy *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 Björk 2019, García 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, Kaarlejärvi *et al* 2015, Vowles *et al* 2017, Ylänne *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, Bråthen *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) 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 decidious 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.
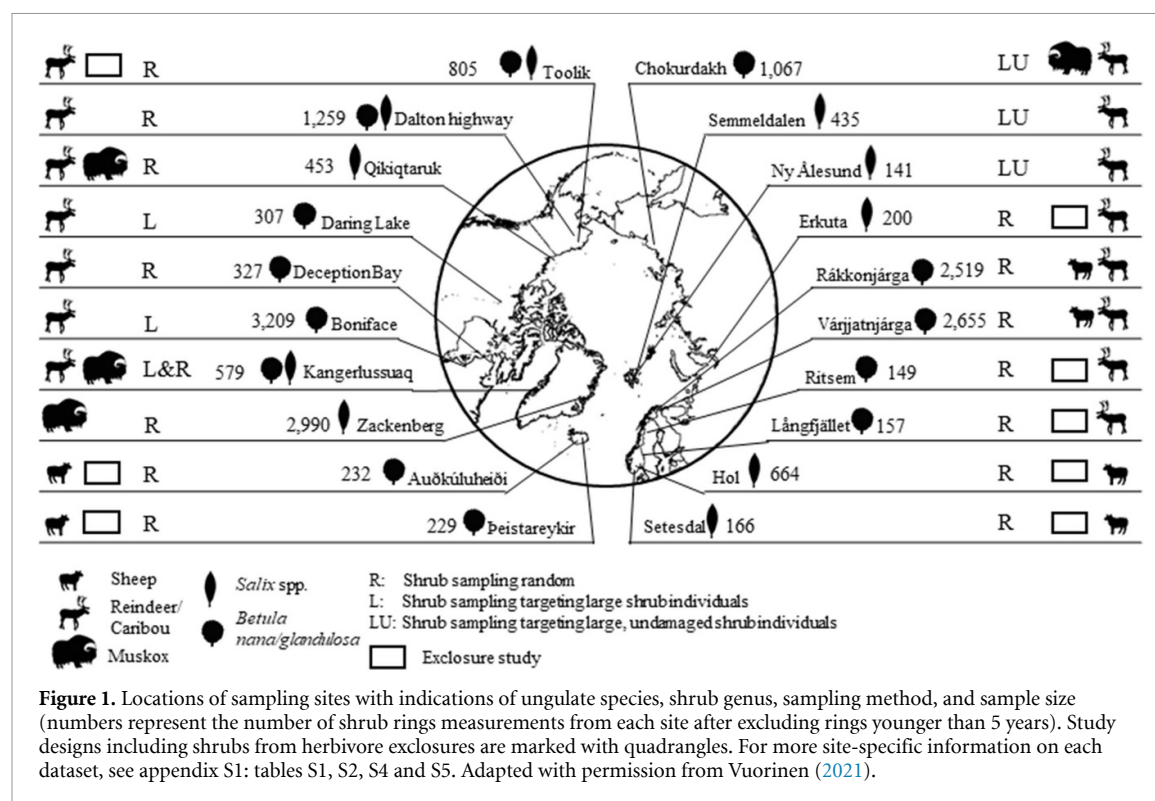
Ring widths were converted to approximation of basal area increment (BAI) by using the dplR-package (Bunn *et al* 2019) to account for geometrical growth trends, assuming that ring circumference can be approximated by a circle (Biondi and Qeadan 2008). While exact area increment measurements are more 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$^{0.75}$, kg km^{-2}). 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

Figure 1. Locations of sampling sites with indications of ungulate species, shrub genus, sampling method, and sample size (numbers represent the number of shrub rings measurements from each site after excluding rings younger than 5 years). Study designs including shrubs from herbivore exclosures are marked with quadrangles. For more site-specific information on each dataset, see appendix S1: tables S1, S2, S4 and S5. Adapted with permission from Vuorinen (2021).

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 ungulate density. Annual biomass values were log-transformed before analyses to homogenize the residual variance.

In addition to the observational ungulate values, experimental ungulate exclosures provided conditions with zero herbivore pressure (see the 'exclosures' 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 ungulate interactions reliably, data needed to be balanced across the captured ungulate density range. To achieve this, we ran two separate analysis: (a) to test the effects of variation in observational ungulate density, and (b) to test the effects of experimental presence-absence of ungulates. In the first analysis, we included only the data points outside of the experimental exclosures. In the second analysis, we only included data from within exclosures and from corresponding open control areas including

only shrub rings grown after the exclosure 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).
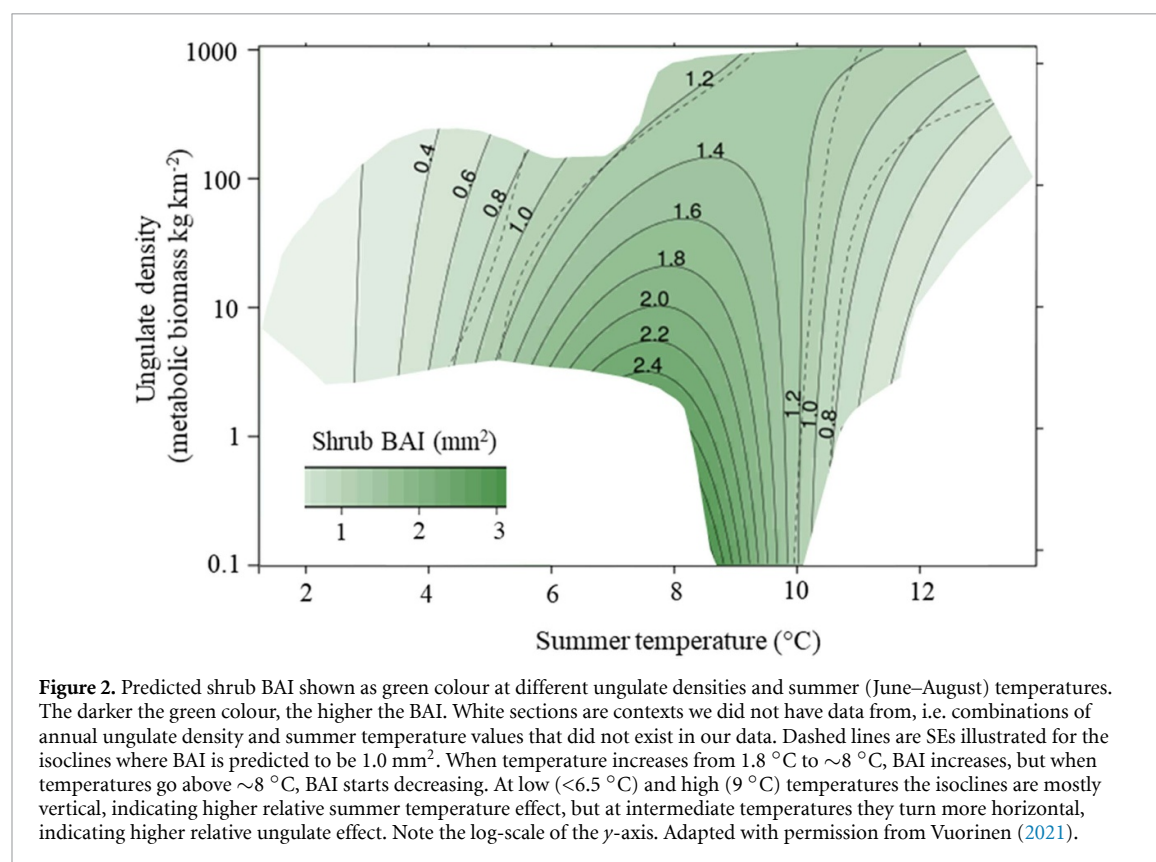
3. Results

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 ∼8 °C and turned slightly negative (table 1, appendix S1: figure S4). Summer temperatures lower than ∼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 exclosure sites, reflecting the relatively short experimental ungulate exclusion periods (13 ± 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^2s (±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 44. Partial R^2s 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 ± 0.1	0.35	−0.23	0.254	1.4	0.1664
Summer temperature	1.1	11 ± 0.9	1.13	0.03	0.107	10.6	<0.0001
Summer temperature^2	—	8.2 ± 0.8	−0.07	−0.60	0.007	−10.3	<0.0001
Ungulate density: summer temperature	—	1.5 ± 0.2	−0.18	0.21	0.060	−3.0	0.0031
Ungulate density: summer temperature^2	—	2.5 ± 0.2	0.01	0.17	0.004	4.0	0.0001
Summer precipitation	1.6	3.8 ± 0.6	0.54	0.39	0.073	7.4	<0.0001
Winter precipitation	1.5	0.1 ± 0.1	0.04	0.05	0.031	1.2	0.24
Age	1.0	5.6 ± 0.7	0.48	0.32	0.014	33.9	<0.0001

Figure 2. Predicted shrub BAI shown as green colour at different ungulate densities and summer (June–August) temperatures. The darker the green colour, the higher the BAI. White sections are contexts we did not have data from, i.e. combinations of annual ungulate density and summer temperature values that did not exist in our data. Dashed lines are SEs illustrated for the isoclines where BAI is predicted to be 1.0 mm^2. When temperature increases from 1.8 °C to ∼8 °C, BAI increases, but when temperatures go above ∼8 °C, BAI starts decreasing. At low (<6.5 °C) and high (9 °C) temperatures the isoclines are mostly vertical, indicating higher relative summer temperature effect, but at intermediate temperatures they turn more horizontal, indicating higher relative ungulate effect. Note the log-scale of the *y*-axis. Adapted with permission from Vuorinen (2021).

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
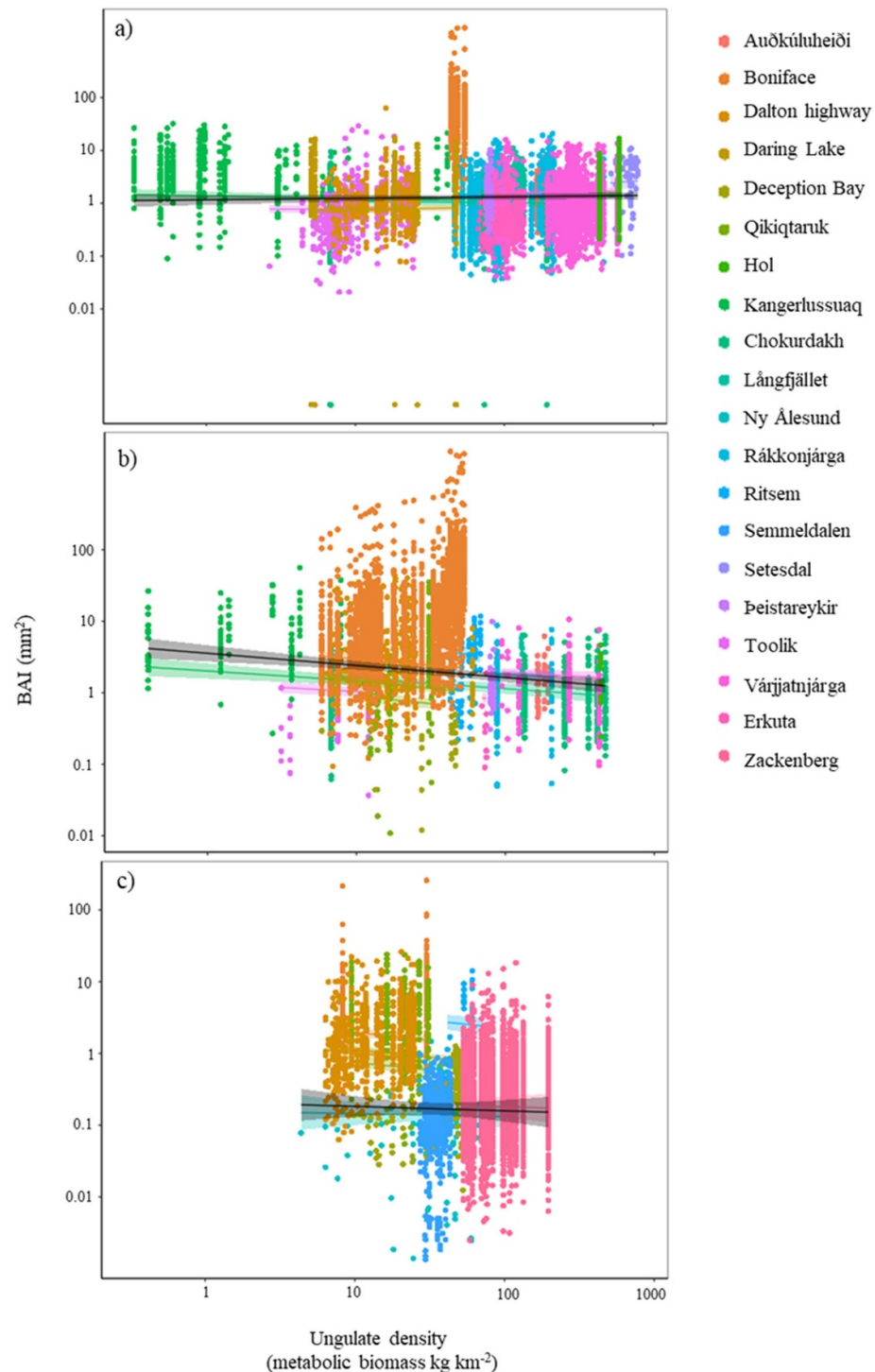
Figure 3. Shrub BAI as a response to annual ungulate density at high (>9 °C; (a)), intermediate (6.5 °C–9 °C; (b)) and low (<6.5 °C; (c)) temperatures. The black prediction lines (±SE) are based on the model prediction under average climatic conditions across the data in the temperature interval in question. In addition, a prediction line has been plotted for each site based on the average climatic conditions on the temperature interval in question. Note that the apparent positive connection between the BAI and ungulate density in raw data from Boniface is likely caused by the collinearity of shrub ring age and ungulate density at that site; this is local collinearity is not expected to distort the overall analysis; see the section 2.

(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 constrains, 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 ~10 °C and at ungulate densities above ~100 kg km^{-2} 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.acuk/cru/data/hrg/cru_ts_4.03/; see also https://catalogue.ceda.acuk/uuid/10d3e3640f 004c578403419aac167d82). 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.k3j 9kd54c, and http://datadryad.org/resource/doi:10.50 61/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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References

Ackerman D *et al* 2017 Arctic shrub growth trajectories differ across soil moisture levels *Glob. Change Biol.* **23** 4294–302

Andruko R *et al* 2020 Recent growth and expansion of birch shrubs across a low Arctic landscape in continental Canada: are these responses more a consequence of the severely declining caribou herd than of climate warming? *Ecosystems* **23** 1362–79

Aune S *et al* 2011 Contrasting climate-and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula *Can. J. For. Res.* **41** 437–49

Berner L T *et al* 2020 Summer warming explains widespread but not uniform greening in the Arctic tundra biome *Nat. Commun.* **11** 1–12

Beumer L T *et al* 2020 An application of upscaled optimal foraging theory using hidden Markov modelling: year-round behavioural variation in a large Arctic herbivore *Mov. Ecol.* **8** 1–16

Biondi F and Qeadan F 2008 A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment *Tree-Ring Res.* **64** 81–96

Bjorkman A D *et al* 2018 Plant functional trait change across a warming tundra biome *Nature* **562** 57–62

Bjorkman A D *et al* 2020 Status and trends in Arctic vegetation: evidence from experimental warming and long-term monitoring *Ambio* **49** 678–92

Bolton D K *et al* 2018 Evidence of vegetation greening at alpine treeline ecotones: three decades of Landsat spectral trends informed by lidar-derived vertical structure *Environ. Res. Lett.* **13** 084022

Bonfils C *et al* 2012 On the influence of shrub height and expansion on northern high latitude climate *Environ. Res. Lett.* **7** 015503

Boscutti F *et al* 2018 Shrub growth and plant diversity along an elevation gradient: evidence of indirect effects of climate on alpine ecosystems *PLoS One* **13** e0196653

Box J E *et al* 2019 Key indicators of Arctic climate change: 1971–2017 *Environ. Res. Lett.* **14** 045010

Bråthen K A *et al* 2017 Rangifer management controls a climate-sensitive tundra state transition *Ecol. Appl.* **27** 2416–27

Bråthen K A and Lortie C 2016 A portfolio effect of shrub canopy height on species richness in both stressful and competitive environments *Funct. Ecol.* **30** 60–69

Bret-Harte M S *et al* 2019. Comparison of the effects of ten years of warming and twenty years of altered plant species composition on ecosystem carbon storage in Alaskan Arctic tundra *AGUFM 2019* pp B11A–07

Bryant J P *et al* 2014 Can antibrowsing defense regulate the spread of woody vegetation in Arctic tundra? *Ecography* **37** 204–11

Buchwal A *et al* 2020 Divergence of Arctic shrub growth associated with sea ice decline *Proc. Natl Acad. Sci.* **117** 33334–44

Bunn A *et al* 2019 Package 'dplR' (available at: https://cran.r-project.org/web/packages/dplR/index.html)

Cahoon S M *et al* 2012a Large herbivores limit CO_2 uptake and suppress carbon cycle responses to warming in West Greenland *Glob. Change Biol.* **18** 469–79

Cahoon S M *et al* 2012b Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets *Ecol. Lett.* **15** 1415–22

Carlson B Z *et al* 2017 Observed long-term greening of alpine vegetation—a case study in the French Alps *Environ. Res. Lett.* **12** 114006

Champagne E *et al* 2012 Tolerance of an expanding subarctic shrub, *Betula glandulosa*, to simulated caribou browsing *PLoS One* **7** e51940

Chapin F S III *et al* 1992 *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective* (New York: Academic)

Christie K S *et al* 2015 The role of vertebrate herbivores in regulating shrub expansion in the Arctic: a synthesis *BioScience* **65** 1123–33

Cohen J *et al* 2013 Effect of summer reindeer grazing on spring snowmelt, albedo and energy balance *Remote Sens. Environ.* **135** 107–17

Cromsigt J P *et al* 2018 Trophic rewilding as a climate change mitigation strategy? *Phil. Trans. R. Soc.* B **373** 20170440

Cuyler C *et al* 2020 Muskox status, recent variation, and uncertain future *Ambio* **49** 805–19

DeFranco K C *et al* 2020 Deeper snow increases the net soil organic carbon accrual rate in moist acidic tussock tundra: ^{210}Pb evidence from Arctic Alaska *Arct. Antarct. Alp. Res.* **52** 461–75

den Herder M *et al* 2008 Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone *Basic Appl. Ecol.* **9** 324–31

Epstein H E *et al* 2008 Phytomass patterns across a temperature gradient of the North American Arctic tundra *J. Geophys. Res.* **113** 1–11

Fisichelli N *et al* 2012 Sapling growth responses to warmer temperatures 'cooled' by browse pressure *Glob. Change Biol.* **18** 3455–63

Gamm C M *et al* 2018 Declining growth of deciduous shrubs in the warming climate of continental western Greenland *J. Ecol.* **106** 640–54

García Criado M *et al* 2020 Woody plant encroachment intensifies under climate change across tundra and savanna biomes *Glob. Ecol. Biogeogr.* **29** 925–43

Graham M H 2003 Confronting multicollinearity in ecological multiple regression *Ecology* **84** 2809–15

Harris I C and Jones P D 2019 CRU TS4.03: climatic research unit (CRU) time-series (TS) version 4.03 of high-resolution gridded data of month-by-month variation in climate (Jan. 19 01 Dec. 2018) *Centre for Environmental Data Analysis* 22 January 2020 (https://doi.org/10.5285/10d3e3640f004c5 78403419aac167d82)

Hofmann R R 1989 Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system *Oecologia* **78** 443–57

Jespersen R G *et al* 2018 Arctic plant ecophysiology and water source utilization in response to altered snow: isotopic (δ^{18}O and δ^{2}H) evidence for meltwater subsidies to deciduous shrubs *Oecologia* **187** 1009–23

Kaarlejärvi E *et al* 2015 Mammalian herbivores confer resilience of Arctic shrub-dominated ecosystems to changing climate *Glob. Change Biol.* **21** 3379–88

Kausrud K *et al* 2006 Density-dependent foraging behaviour of sheep on alpine pastures: effects of scale *J. Zool.* **270** 63–71

Le Moullec M *et al* 2020 Climate synchronises shrub growth across a high-arctic archipelago: contrasting implications of summer and winter warming *Oikos* **129** 1012–27

Le Moullec M, Buchwal A, Wal R, Sandal L, Hansen B B and Jucker T 2019 Annual ring growth of a widespread high arctic shrub reflects past fluctuations in community-level plant biomass *J Ecol* **107** 436–51

Leffler A J *et al* 2016 Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra *Oecologia* **181** 287–97

Li B *et al* 2016 The role of summer precipitation and summer temperature in establishment and growth of dwarf shrub *Betula nana* in northeast Siberian tundra *Polar Biol.* **39** 1245–55

Macias-Fauria M *et al* 2014 Spatiotemporal patterns of warming *Nat. Clim. Change* **4** 845–6

Macias-Fauria M *et al* 2020 Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? *Phil. Trans. R. Soc.* B **375** 20190122

May J L *et al* 2017 Short-term impacts of the air temperature on greening and senescence in Alaskan Arctic plant tundra habitats *Remote Sens.* **9** 1338

Morrissette-Boileau C *et al* 2018 Revisiting the role of migratory caribou in the control of shrub expansion in northern Nunavik (Québec, Canada) *Polar Biol.* **41** 1845–53

Mosbacher J B *et al* 2019 Muskoxen modify plant abundance, phenology, and nitrogen dynamics in a High Arctic fen *Ecosystems* **22** 1095–107

Myers-Smith I H *et al* 2015a Climate sensitivity of shrub growth across the tundra biome *Nat. Clim. Change* **5** 887–91

Myers-Smith I H *et al* 2015b Methods for measuring Arctic and alpine shrub growth: a review *Earth-Sci. Rev.* **140** 1–13

Myers-Smith I H *et al* 2020 Complexity revealed in the greening of the Arctic *Nat. Clim. Change* **10** 106–17

Myers-Smith I H and Hik D S 2018 Climate warming as a driver of tundra shrubline advance *J. Ecol.* **106** 547–60

Naito A T and Cairns D M 2011 Patterns and processes of global shrub expansion *Prog. Phys. Geogr.* **35** 423–42

Nicholson K L *et al* 2016 Modeling caribou movements: seasonal ranges and migration routes of the Central Arctic herd *PLoS One* **11** e0150333

Niskanen A K *et al* 2017 Drivers of high-latitude plant diversity hotspots and their congruence *Biol. Conserv.* **212** 288–99

Oksanen T *et al* 2020 The impact of thermal seasonality on terrestrial endotherm food web dynamics: a revision of the exploitation ecosystem hypothesis *Ecography* **43** 1859–77

Olesen C R *et al* 1994 Growth of wild muskoxen under two nutritional regimes in Greenland *Rangifer* **14** 3–10

Olofsson J *et al* 2004 Reindeer influence on ecosystem processes in the tundra *Oikos* **105** 386–96

Olofsson J *et al* 2009 Herbivores inhibit climate-driven shrub expansion on the tundra *Glob. Change Biol.* **15** 2681–93

Olofsson J and Post E 2018 Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding *Phil. Trans. R. Soc.* B **373** 20170437

Pajunen A *et al* 2012 Browsing-mediated shrub canopy changes drive composition and species richness in forest-tundra ecosystems *Oikos* **121** 1544–52

Pedersen S H *et al* 2021 Quantifying effects of snow depth on caribou winter range selection and movement in Arctic Alaska *Mov. Ecol.* **9** 1–24

Phoenix G K and Bjerke J W 2016 Arctic browning: extreme events and trends reversing arctic greening *Glob. Change Biol.* **22** 2960–2

Pinheiro J *et al* 2017 Package 'nlme'. Linear and nonlinear mixed effects models, version 3

Plante S *et al* 2014 Shrub cover in northern Nunavik: can herbivores limit shrub expansion? *Polar Biol.* **37** 611–9

Post E and Pedersen C 2008 Opposing plant community responses to warming with and without herbivores *Proc. Natl Acad. Sci.* **105** 12353–8

Prendin A L *et al* 2020 Immediate and carry-over effects of insect outbreaks on vegetation growth in West Greenland assessed from cells to satellite *J. Biogeogr.* **47** 87–100

Prevéy J S *et al* 2019 Warming shortens flowering seasons of tundra plant communities *Nat. Ecol. Evol.* **3** 45–52

Ravolainen V T *et al* 2014 Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra *J. Appl. Ecol.* **51** 234–41

Richert J *et al* 2021 Snowier winters extend autumn availability of high-quality forage for caribou in Arctic Alaska *Ecosphere* **12** e03617

Ropars P, Lévesque E, Boudreau S and Bardgett R 2015 How do climate and topography influence the greening of the forest-tundra ecotone in northern Québec? A dendrochronological analysis of Betula glandulosa *J Ecol* **103** 679–90

Ross L C *et al* 2016 Sheep grazing in the North Atlantic region: a long-term perspective on environmental sustainability *Ambio* **45** 551–66

Schimel J P *et al* 2004 Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities *Soil Biol. Biochem.* **36** 217–27

Schmidt N M *et al* 2016 Ungulate movement in an extreme seasonal environment: year-round movement patterns of high-arctic muskoxen *Wildlife Biol.* **22** 253–67

Skarin A *et al* 2020 Reindeer use of low Arctic tundra correlates with landscape structure *Environ. Res. Lett.* **15** 115012

Speed J D *et al* 2010 Experimental evidence for herbivore limitation of the treeline *Ecology* **91** 3414–20

Speed J D *et al* 2013 The response of alpine *Salix* shrubs to long-term browsing varies with elevation and herbivore density *Arct. Antarct. Alp. Res.* **45** 584–93

Speed J D *et al* 2014 Long-term increase in aboveground carbon stocks following exclusion of grazers and forest establishment in an alpine ecosystem *Ecosystems* **17** 1138–50

Speed J D *et al* 2019 Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time *PLoS One* **14** e0217166

Speed J D *et al* 2021 Will borealization of Arctic tundra herbivore communities be driven by climate warming or vegetation change? *Glob. Change Biol.* **27** 6568–77

Sturm M *et al* 2005 Changing snow and shrub conditions affect albedo with global implications *J. Geophys. Res.* **110** 1–13

Virtanen R *et al* 2016 Where do the treeless tundra areas of northern highlands fit in the global biome system: toward an ecologically natural subdivision of the tundra biome *Ecol. Evol.* **6** 143–58

Vors L S and Boyce M S 2009 Global declines of caribou and reindeer *Glob. Change Biol.* **15** 2626–33

Vowles T *et al* 2016 The impact of shrub browsing by mountain hare and reindeer in subarctic Sweden *Plant Ecol. Divers.* **9** 421–8

Vowles T *et al* 2017 Expansion of deciduous tall shrubs but not evergreen dwarf shrubs inhibited by reindeer in Scandes mountain range *J. Ecol.* **105** 1547–61

Vowles T and Björk R G 2019 Implications of evergreen shrub expansion in the Arctic *J. Ecol.* **107** 650–5

Vuorinen K E *et al* 2017 Open tundra persist, but arctic features decline—vegetation changes in the warming Fennoscandian tundra *Glob. Change Biol.* **23** 3794–807

Vuorinen K E *et al* 2020a Cool as a moose: how can browsing counteract climate warming effects across boreal forest ecosystems? *Ecology* **101** e03159

Vuorinen K E *et al* 2020b Herbivory and climate as drivers of woody plant growth: do deer decrease the impacts of warming? *Ecol. Appl.* **30** e02119

Vuorinen K E 2021. When do ungulates override the climate? Defining the interplay of two key drivers of northern vegetation dynamics *Doctoral Theses* (Trondheim: Norwegian University of Science and Technology, Faculty of Natural Sciences, Department of Biology) p 119

Welker J M *et al* 1993 Leaf carbon isotope discrimination and vegetative responses of *Dryas octopetala* to temperature and water manipulations in a High Arctic polar semi-desert, Svalbard *Oecologia* **95** 463–9

Welker J M *et al* 2004 Alpine grassland CO_2 exchange and nitrogen cycling: grazing history effects, medicine bow range, Wyoming, USA *Arct. Antarct. Alp. Res.* **36** 11–20

Welker J *et al* 2005 Leaf mineral nutrition of Arctic plants in response to warming and deeper snow in northern Alaska *Oikos* **109** 167–77

Ylänne H *et al* 2018 Consequences of grazer-induced vegetation transitions on ecosystem carbon storage in the tundra *Funct. Ecol.* **32** 1091–102

Yu Q *et al* 2017 Circumpolar Arctic tundra biomass and productivity dynamics in response to projected climate change and herbivory *Glob. Change Biol.* **23** 3895–907