


# Climate warming impacts tuttuk (caribou) forage availability in Tongait (Torngat) Mountains, Labrador

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## Abstract

Tuttuk (caribou (*Rangifer tarandus*)) populations are in decline across Canada, making them a major conservation concern for Inuit of Nunatsiavut (Northern Labrador) and Nunavik (Northern Quebec). This study investigates changes to caribou forage over 14 years at two tundra sites in northern Nunatsiavut, Labrador. We ask: (1) How much of the total vegetation is suitable caribou forage and how has this changed with time and experimental warming; and (2) which forage species are most affected by recent climate change? At control and warming plots, we identified selected, edible, and avoided caribou forage based on published literature, and modeled observed changes in forage availability. We found that the relative frequency of selected winter forage was lower than summer forage at both sites. Caribou appear to be more forage limited in the winter than summer, and birch (*Betula* spp.), and ericaceous shrub species (*Vaccinium* spp.), increased over time. Our research provides valuable insight into recent changes in caribou forage availability and develops a novel methodology that can be applied across other caribou ranges. This knowledge will inform conservation and management measures by helping identify possible forage limitations and can contribute to recovery targets across Nunatsiavut and ultimately the social-ecological resilience of northern communities.

**Key words:** climate change, Labrador, Arctic, Nunatsiavut, caribou

## Introduction

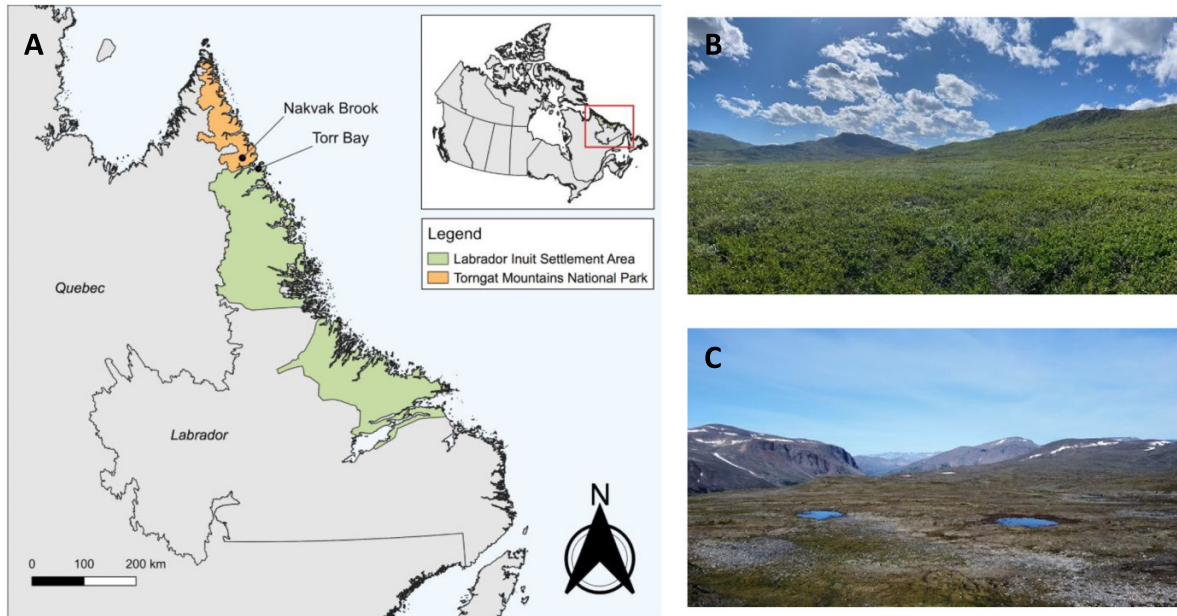
Canada's Arctic and Subarctic regions are experiencing dramatic environmental change, with changes in surface air temperature occurring at up to four times the average global rate (Ballinger et al. 2020; Rantanen et al. 2022). Consequences of warming Arctic air temperatures include sea ice loss, glacial melt, permafrost thaw, and changes in vegetation growth and composition (Lawrence et al. 2008; Elmendorf et al. 2012; Koven et al. 2013; Meredith et al. 2019). These changes have serious implications for the people, plants, and wildlife who inhabit the North (Ford et al. 2019; Meredith et al. 2019; Hancock et al. 2022).

For Inuit living in northern Labrador (Nunatsiavut) and northern Quebec (Nunavik), caribou (*Rangifer tarandus*; tuttuk in Nunatsiavut) are a cultural keystone species with intangible value far beyond being a food source (Brice-Bennett et al. 1977; Cristancho and Vining 2004; Garibaldi and Turner 2004; Borish et al. 2021). Over the past three decades, the migratory George River caribou (GRC) herd, whose range extends into the Torngat Mountains, has experienced a drastic population decline from 770 000 caribou in 1993 (Couturier et al. 1996) to 5500 in 2018 (Bongelli et al. 2022), but, by 2022,

has increased to 7200 individuals (Government of Newfoundland and Labrador 2022). Further, recent population surveys of the montane Torngat Mountains caribou (TMC) population showed small but increasing population numbers (~1326 caribou in 2017) (Couturier et al. 2015, 2018). Due to low herd sizes, in January 2013, the Government of Newfoundland and Labrador implemented a hunting ban on the GRC herd that has negatively impacted Inuit wellbeing and cultural continuity (Cunsolo et al. 2020; Snook et al. 2020; Borish et al. 2021). Understanding and co-managing these herds in the face of a rapidly changing Arctic will be crucial for the long-term prosperity of caribou, Inuit and Labrador Innu who also use this region (Borish et al. 2021; Ward et al. 2021).

Coinciding with changes in caribou populations, Arctic warming has been accompanied by the expansion of deciduous shrubs into tundra landscapes (Sturm et al. 2001; Fraser et al. 2014). Increases in shrub biomass, abundance, and cover across Arctic ecosystems have been colloquially termed "shrubification" (Myers-Smith et al. 2011). Evidence of shrubification has been identified through Inuit Knowledge (Wilson et al. 2014; Cuerrier et al. 2015; Siegwart Collier 2020), historical photographs (Sturm et al. 2001; Tremblay et al. 2012),

**Fig. 1.** (A) A map of the study sites in Nunatsiavut, Canada, (B) Torr Bay study site, and (C) Nakvak Brook study site. Map was created with NAD83 projections and UTM coordinate system. Data used for map includes: Canada boundary (Statistics Canada 2021); Labrador Inuit Settle Area boundary (Government of Canada 2023); Torngat Mountains National Park boundary (Government of Canada 2015).



remote sensing (Fraser et al. 2011; Davis et al. 2021b), dendrochronology (Ackerman et al. 2018; Larking et al. 2021), and vegetation surveys (Elmendorf et al. 2012; Bjorkman et al. 2018). A major consequence of shrubification is that greater shrub cover can shade out lichens, reducing their abundance and species richness (Elmendorf et al. 2012; Fraser et al. 2014; Alatalo et al. 2017; Chagnon and Boudreau 2019). A loss of lichen abundance has serious ramifications for caribou, whose winter diets are generally composed of greater than 50% mat-forming lichens (Thomas and Hervieux 1986; Heggberget et al. 2002; Joly and Cameron 2018; Webber et al. 2022). Conversely, important spring and summer caribou forage, such as birch (*Betula* spp.), willow (*Salix* spp.), and ericaceous (*Vaccinium* spp.) shrub species, are expanding in some areas with climate warming (Denryter et al. 2017; Ehlers et al. 2021; Webber et al. 2022).

Despite significant complexities surrounding the effects of climate warming on the abundance of caribou forage, a comprehensive assessment of these effects on montane caribou herds has yet to be completed. Montane caribou often have smaller forage areas compared to migratory caribou, thus there is an even greater need to understand patterns of forage availability (Bergerud et al. 2007). Our study investigates changes to caribou forage availability due to ambient and experimental warming at two tundra sites located within the range of the TMC population. The objective of our study is to address the following questions: (1) What relative frequency of total vegetation is suitable for summer and winter caribou forage, and how has this changed with time and experimental warming in mountainous coastal tundra? (2) Which forage species are most affected by recent climate warming? To answer these questions, we analyze point-frame vegetation data

collected during a 14 year study within Torngat Mountains National Park (*Tongait KakKasuangita SilakKijapvinga* in Inuttitut; TMNP). Based on Arctic warming and shrub expansion trends, we expect to see an increase in summer caribou forage since deciduous shrubs are primary summer forage. We also expect to see a decline in winter forage since lichens are primary winter forage and fast-growing shrubs can out-compete lichen. Our approach of analyzing changes to plant communities from the perspective of caribou forage can be applied in any northern region with knowledge of caribou forage.

## Study sites

Torngat Mountains National Park is cooperatively managed by members of the Nunatsiavut Government, Makivik Corporation, and Parks Canada (all of whom are Inuit from Nunatsiavut and Nunavik). Data collection was undertaken at Torr Bay (58.46°N, 62.82°W; 40 m above sea level) and Nakvak Brook (*Pitukkik* in Inuttitut) (58.64°N, 63.35°W; 420 m above sea level) which are both located in Nunatsiavut and are near the southern portion of *Tongait KakKasuangita SilakKijapvinga*/Torngat Mountains National Park (Fig. 1). These study sites were established in 2009 and 2007, respectively, and have been re-sampled periodically to monitor vegetation change in the region (Siegwart Collier 2020). Overall, TMNP is dominated by dry vegetation land cover (61.3%; of which 21.7% is herb-lichen tundra), followed by wet vegetation (18.8%; of which 57.7% is moist sedge) and shrub cover (6.5%; of which 28.5% is dwarf shrub and 58.7% is low-medium shrub) (Davis et al. 2021b). The area surrounding Torr Bay has been identified as an especially important caribou hunting

ground for Inuit (Wilson et al. 2014). Torr Bay is located in a mesic, low-shrub, tundra environment, and is characterized by deciduous shrub species with very little lichen cover. Study plots are distributed on both sides of a river valley. The shrub canopy is dominated by dwarf birch (*Betula glandulosa* Michx; AvaᓃlaKiak) with some willow species (*Salix herbacea* L.; Dwarf willow, and *S. arctica* Pall; UKaujajak; Arctic willow) while the ground cover is composed mainly of dwarf ericaceous shrubs (*Vaccinium uliginosum* L./Kigutanginnak/bog bilberry, *V. vitis-idaea* subsp. minus L./Kimminak/redberry, *Empetrum nigrum* L./Paungak/crowberry, *Rhododendron tomentosum* L./Mamaittukuluk/marsh Labrador tea, and *Rhododendron groenlandicum* Oeder./MamaittuKotet/Labrador tea).

Nakvak Brook is located in an upland basin at the base of a mountain but is flatter, more open, and has far less shrub cover than the Torr Bay site. Nakvak Brook is primarily composed of low-tundra vegetation, small wetlands, and exposed rock. The shrub canopy at Nakvak Brook is dominated by prostrate *Salix* species (*S. arctica*, *S. herbacea*, *S. pedicellaris* Pursh.; bog willow, and *S. uva-ursi* Pursh.; bearberry willow) with some dwarf birch and bog bilberry present. Ground cover in the dry areas tends to have a greater abundance of lichen (*Cladonia* spp., *Flavocetraria* spp., and *Stereocaulon* spp.) and evergreen shrubs, whereas mosses and graminoids are more common in wet areas. Visual observations and limited soil moisture measurements at the site suggest that wet areas have undergone a drying trend in the last decade (Davis et al. 2021a). At both the Torr Bay and Nakvak Brook sites, recent caribou herbivory is presumed to be low due to a locally small, but increasing, caribou population.

Atmospheric reanalysis data (Hersbach et al. 2020), down-scaled following Davis et al. (2021a) for our two sites, indicate that mean temperatures of the coldest and warmest months are  $-22\text{ }^{\circ}\text{C}$  (February) and  $9\text{ }^{\circ}\text{C}$  (August) at Torr Bay, and  $-25\text{ }^{\circ}\text{C}$  (February) and  $8\text{ }^{\circ}\text{C}$  (July) at Nakvak Brook (1989–2018 climate normals). Mean winter and summer regional temperatures have increased by  $2.0\text{ }^{\circ}\text{C}/\text{decade}$  and  $0.5\text{ }^{\circ}\text{C}/\text{decade}$ , respectively, over the past 30 years (Barrette et al. 2020). Permafrost in the region is widespread though field observations are limited (Way and Lewkowitz 2016).

## Methods

### Study design

Study sites were established at Torr Bay and at Nakvak Brook during the summers of 2009 and 2007, respectively. Subsets of this dataset has been used in other publications by Davis et al. (2021a) and Siegwart Collier (2020). At each site, paired experimental warming and control plots were established (Torr Bay,  $N = 30$ ; Nakvak Brook,  $N = 19$ ). At Torr Bay, plots were equally dispersed on East and West facing slopes on either side of Torr Bay Pond over an area of  $1.8\text{ km}^2$ , while at Nakvak Brook, plots were divided between Wet and Dry subsites over a smaller area ( $0.36\text{ km}^2$ ). When the experiment was initiated, the locations of the Wet plots were selected by the presence of saturated soils (and in some cases, standing water), whereas the Dry plots had drier soils (see Davis et al.

2021a for limited soil moisture data). Plots were resampled in 2011 and 2016 at Torr Bay, and in 2010, 2015, and 2021 at Nakvak Brook, to understand the effects of ambient warming, by comparing control plots through time, and experimental warming, by comparing warmed and control plots through time, on vegetation composition and abundance. At both sites over the period of study, foraging by caribou was uncommon (L. Hermanutz, pers. comm.) with a recent population survey reporting a slight increase of individuals in our study area (Couturier et al. 2015, 2018).

Study design and data collection methods followed the protocols developed for the International Tundra Experiment (ITEX; <https://ibis.geog.ubc.ca/itex/>). Data on changes in vegetation (which includes plant, lichen, and moss species) composition and abundance were collected through point-frame vegetation surveys. The point-frame plots at Torr Bay measure  $70\text{ cm} \times 70\text{ cm}$ , while those at Nakvak Brook measure  $1\text{ m} \times 1\text{ m}$ . Vegetation data were collected using a gridded frame with  $10\text{ cm}$  grids, resulting in 70 and 100 data collection points per plot, respectively, for Torr Bay and Nakvak Brook. During the point-frame process, at each intersection, the height and species identification for all species making contact with the point-frame pin were recorded, so more than 70 or 100 species could be listed for each plot depending on the vertical structure of the plant community. Plants, lichens and mosses were identified to species level whenever possible; however, some could only be identified to genus, or lifeform type. Generally, most monocots and dicots were identified to the species level, but mosses and lichens were commonly identified to genus.

To simulate changes in vegetation resulting from tundra warming, open-top chambers (OTCs) were established (paired with a control plot with 5–30 m apart in comparable microsite conditions) to warm vegetation and shelter it from the wind, also moderating diurnal heat loss. OTCs are considered an appropriate analogue for regional climate warming (Hollister and Webber 2000; Henry et al. 2022), and are estimated to increase mean daily summer air temperatures by  $1.5\text{ }^{\circ}\text{C}$  and soil temperatures by  $1.0\text{ }^{\circ}\text{C}$  (Elmendorf et al. 2012). At the Torr Bay site, OTCs were found to raise mean daily summer soil temperatures by approximately  $1.5\text{--}2\text{ }^{\circ}\text{C}$  compared to the control plot soil temperatures (Siegwart Collier 2020). The Climate Atlas of Canada (2019) projects that summer (June, July, and August; JJA) temperatures will increase approximately  $1.5\text{ }^{\circ}\text{C}$  by 2050 in northern Nunatsiavut, therefore, OTCs are an appropriate tool to replicate climate warming in our study.

### Ranking caribou forage

To assess changes in caribou forage between control and warmed plots, and changes throughout the course of this study, relative frequency and abundance, we had to first identify which vegetation species found in our plots were caribou forage and to what extent. To do this, we reviewed the literature on caribou forage and used published literature that identified forage types to the species or genus level. These papers were then included in our rank



calculations. In total, 20 papers were included (see list in Supplemental Material B). Species ranks of 0, 1, and 2 were assigned to each species listed in the selected papers (see Table 1). A rank of “0” was assigned to species that were avoided by caribou, a rank of “1” for species that were edible but not selected for by caribou, and a rank of “2” was assigned for selected forage species. We used the term “selected”, rather than “preferred” as determining preference would require forage being equally available, a scenario that would only be possible in a controlled cafeteria experiment. Ranks were based on each species’ relative frequency in rumen, scat, or visual forage recordings in comparison to other species in each study. Finally, overall forage ranks were assigned to each species based on their most common ranking across papers for each season. Any species that were identified in our plots but did not appear in the forage literature assumed a rank of “0” (i.e., not an important forage species).

### Statistical analyses

To answer our first research question: what relative frequency of total vegetation is suitable summer and winter caribou forage, and how has this changed with time and experimental warming? We created a table comparing the relative frequency (calculated as the number of times a forage ranking was intercepted in a plot relative to the total number of intercepts) of vegetation from each forage ranking (0, 1, and 2) in our control and OTC plots across the duration of the study. We then explored how the abundance of avoided, edible, and selected forage rankings have changed with time and experimental warming at both sites across winter and summer periods. An example of avoided, edible, and selected summer and winter forage for control and experimentally warmed plots is shown in Fig. 2. A complementary approach was used to evaluate our second research question: of the selected forage species, which are most affected by recent climate warming? In this analysis, we modeled the effects of time and experimental warming on the abundance (species count per site) of six highly-selected forage genera and the lifeform of lichens.

We used GLMMs to analyze the effects of time (Torr Bay 2009 vs. 2016 and Nakvak Brook 2010 vs. 2021), experimental warming (OTC vs. control), and subsite (Torr Bay East facing vs. West facing, and Nakvak Brook Wet vs. Dry) on the relative frequency of avoided, edible, and selected summer and winter caribou forage, as well as the abundance of the selected forage species and a lichen lifeform model. As lichens are a very important forage group for caribou, especially in the winter, a general lichen model was included. Using a lichen lifeform approach, rather than selected genera, was necessary as many lichens could not be identified to the species level or had low abundance, and using *Cladonia* or *Stereocaulon* only models may have led to an underestimation of lichen abundance at our sites. We used a mixed effect modeling approach as our study design involved repeat sampling of the same plots at multiple points in time (Zuur et al. 2009;

Elmendorf et al. 2012). The mixed effect model also allowed us to include plot numbers as random effects to account for paired OTC and control plots.

Due to the large number of models needed for forage ranks ( $N = 12$ ) and forage genera ( $N = 14$ ), and because models could consist of various combinations of main effects, distributions, and model types, we followed an approach used by Brooks et al. (2017) to select the most parsimonious model from numerous model types and parameters. The approach we applied first fits data to GLMMs with each combination of main effects, distribution, and model type and then uses the Akaike Information Criteria (AIC) to compare the fit of the various model options.

To select appropriate model parameters for the forage rank and genera level analyses, we first fit GLMMs, and zero-inflated GLMMs to the dataset, respectively, with log-linked Poisson and negative binomial distributions. To account for overdispersion, common with count data, we ran zero-inflated models for the genera level analyses as there were many plots where a genus was absent resulting in high counts of zero (Zuur et al. 2009). Furthermore, each model type and distribution we tested also contained different combinations of interaction functions for the three fixed effects (Treatment, Year, and Subsite). Every model included abundance as the response variable and plot as a random effect.

For the forage rank GLMMs, a total of six models were run for each seasonal forage rank for each site. We did not consider zero-inflated models as an option for the forage rank models since an excess number of zeros did not appear in any histograms of the count data. For analyzing forage genera, 16 model combinations were considered for each selected forage genus at the Torr Bay site and 12 models were run for each selected forage genus at the Nakvak Brook site (Supplemental Material A Tables S2). A priori, we expected the Wet/Dry subsite to have a stronger influence on genera abundance than the East facing/West facing subsite effect at Torr Bay, so subsite was always included in the Nakvak Brook models, which explains why fewer model combinations were explored.

We then used the AIC to compare the models. We identified the models with the three lowest AIC values for each forage rank and for each genus and from those we selected the model that best fit the majority of ranks or genera (Supplemental Material A Tables S1 and S2). Since we wanted to compare results across ranks, and between genera we had to use the same model for all ranks and all genera at each site. This meant that we could not simply select the model with the lowest AIC value for each rank and genera. In total, this approach left us with the possibility of using four different model structures in our analysis.

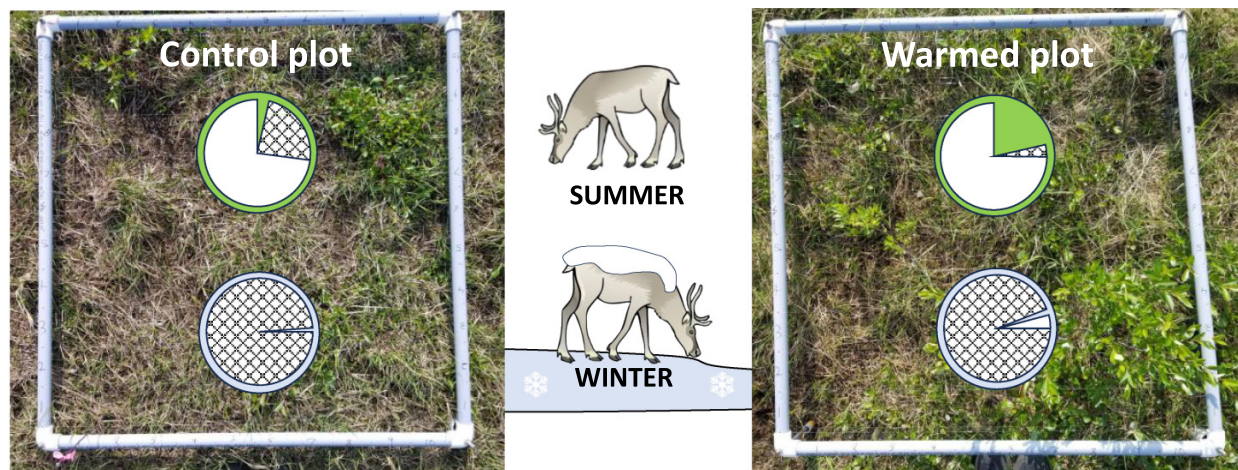
Since our OTC treatment plots at time zero are expected to be the same as our control plots at time zero (i.e., the warming treatment had not yet been applied), we did not expect to find any significant results from our treatment (OTC) main effect. Regardless, we chose to include treatment as a main effect to determine interaction effects, which could indicate how abundance is changing through time in treatment plots compared to control plots. This decision is in line with the hierarchy principle that dictates insignificant terms should

**Table 1.** Selected caribou forage species present in the Torngat Mountains Region of Labrador, Canada, as identified through an extensive literature search and expert knowledge (see Methods for details on how this table was generated).

Winter forage species	Winter forage functional type	Winter forage references	Summer forage species	Summer forage functional type	Summer forage references
<i>Alectoria ochroleuca</i>	Lichen	Bergerud (1972); Gauthier et al. (1989)	<i>Alectoria ochroleuca</i>	Lichen	Gauthier et al. (1989); Pitcher (2012); Denryter et al. (2017)
<i>Cetraria islandica</i>	Lichen	Bergerud (1972); Gaare and Skogland (1975); Miller (1976); Thomas and Hervieux (1986); Gauthier et al. (1989); Côté (1998)	<i>Betula glandulosa</i>	Deciduous shrub	Gauthier et al. (1989); Ehlers et al. (2021)
<i>Cladonia arbuscula</i>	Lichen	Skoog (1968); Bergerud (1972); Pitcher (2012);	<i>Carex bigelowii</i>	Sedge	Skoog (1968); Boertje (1985); Manseau et al. (1996); Lenart et al. (2002)
<i>Cladonia deformis</i>	Lichen	Bergerud (1972)	<i>Carex rariflora</i>	Sedge	Côté (1998)
<i>Cladonia mitis</i>	Lichen	Bergerud (1972); Gaare and Skogland (1975); Pitcher (2012)	<i>Carex rotundifolia</i>	Sedge	*
<i>Cladonia rangiferina</i>	Lichen	Skoog (1968); Bergerud (1972); Pitcher (2012)	<i>Carex</i> spp.	Sedge	Skoog (1968); Bergerud (1972); Gaare and Skogland (1975); Shank et al. (1978); Boertje (1985); Gauthier et al. (1989); Ehlers et al. (2021)
<i>Cladonia stellaris</i>	Lichen	Skoog (1968); Bergerud (1972); Côté (1998); Pitcher (2012)	<i>Cetraria islandica</i>	Lichen	*
<i>Cladonia uncialis</i>	Lichen	Skoog (1968); Bergerud (1972); Pitcher (2012)	<i>Cladonia arbuscula</i>	Lichen	*
<i>Equisetum arvense</i>	Horsetail	Boertje (1985); Miller (1976)	<i>Cladonia deformis</i>	Lichen	*
<i>Flavocetraria cucullata</i>	Lichen	Skoog (1968); Gaare and Skogland (1975)	<i>Cladonia mitis</i>	Lichen	Denryter et al. (2017)
<i>Flavocetraria nivalis</i>	Lichen	Skoog (1968); Gaare and Skogland (1975)	<i>Cladonia rangiferina</i>	Lichen	Denryter et al. (2017); Ehlers et al. (2021)
<i>Gowardia nigricans</i>	Lichen	Bergerud (1972)	<i>Cladonia stellaris</i>	Lichen	*
<i>Stereocaulon</i> spp.	Lichen	Miller (1976); Thomas and Hervieux (1986); Gauthier et al. (1989); Côté (1998)	<i>Equisetum arvense</i>	Horsetail	Boertje (1985); Christopherson et al. (2019); Ehlers et al. (2021)
<i>Vaccinium vitis-idaea</i>	Evergreen shrub	Bergerud (1972); Miller (1976); Boertje (1985); Gauthier et al. (1989)	<i>Flavocetraria cucullata</i>	Lichen	Denryter et al. (2017); Ehlers et al. (2021)
			<i>Flavocetraria nivalis</i>	Lichen	Denryter et al. (2017); Ehlers et al. (2021)
			<i>Salix arctica</i>	Deciduous shrub	Shank et al. (1978); Boertje (1985); Lenart et al. (2002); Bergerud et al. (2007)
			<i>Salix glauca</i>	Deciduous shrub	*
			<i>Salix herbacea</i>	Deciduous shrub	Manseau et al. (1996)
			<i>Salix pedicellaris</i>	Deciduous shrub	*
			<i>Salix uva-ursi</i>	Deciduous shrub	Manseau et al. (1996); Bergerud et al. (2007)
			<i>Vaccinium uliginosum</i>	Deciduous shrub	Bergerud (1972); Boertje (1985); Gauthier et al. (1989); Crete et al. (1990); Manseau et al. (1996); Côté (1998); Bergerud et al. (2007); Denryter et al. (2017); Christopherson et al. (2019); Ehlers et al. (2021)
			<i>Vaccinium vitis-idaea</i>	Evergreen shrub	Bergerud (1972); Boertje (1985); Gauthier et al. (1989); Zamin et al. (2017); Christopherson et al. (2019)

\*Species were included in selected summer forage list without reference based on difficulty of identifying species in gut analyses (i.e., *Carex* spp. and *Salix* spp.) and overall importance to diet (i.e., *Cladonia* spp.)

**Fig. 2.** Representation of caribou forage for both control (left) and experimentally warmed (right) plots. For summer forage in control plot (top left), 71% of the plot was selected (white), 23% were avoided (hashed), and 7% (empty) was edible but not considered important summer forage. For winter forage in control plot (bottom left), 0% of the plot was selected, 99% were avoided, and 1% was edible but not considered important winter forage. For summer forage in experimentally warmed plot (top right), 75% of the plot was selected forage, 5% were avoided, and 20% was edible, while winter forage in experimentally warmed plot (bottom right) represented 5% of the plot was selected, 95% were avoided, and less than 1% was edible.



be included in the model if they help to satisfy the goals of the experiment (Montgomery et al. 2005).

All generalized linear mixed models were analyzed in R version 4.1.2 (The R Core Team 2021) using the package glmmTMB (Magnusson et al. 2017). Effect plots were constructed using packages SjPlot (Lüdecke et al. 2021), and ggplot2 (Wickham 2016).

## Results

### Compiled caribou forage

Through an extensive literature search (Supplemental Material B), we identified 14 selected winter, and 21 selected summer, forage species at our sites (Table 1). This literature search highlighted the importance of lichens, especially *Cladonia* spp., as a winter food source (Bergerud 1972; Thomas and Hervieux 1986; Gauthier et al. 1989), while leafy deciduous species such as birch, willow, and blueberry (*Vaccinium* spp.) made up a large portion of a caribou's summer diet (Denryter et al. 2017; Ehlers et al. 2021; Webber et al. 2022). A caribou's spring diet was found to have a high composition of sedge species (*Carex* spp.) (Bergerud 1972; Gauthier et al. 1989; Béland 2022). Overall, winter forage was less diverse than summer forage, and mainly composed of lichen species.

### Caribou forage ranks

The relative frequency of avoided, edible, and selected forage found in the study's control and OTC plots showed that the forage rank with the greatest relative frequency in the summer is the selected rank while in the winter it is the edible but not selected rank for Torr Bay, and the avoided rank for Nakvak Brook (Table 2). Overall, the relative frequency of selected winter caribou forage is much lower than the relative frequency of selected summer forage across both plot

types at both sites. In the control plots at Torr Bay, selected winter forage increased significantly from 2009 to 2016 ( $p < 0.01$ ) (Table 2; Supplemental Material A Tables S7 and S8). In the OTC plots, selected winter forage declined significantly from 2010 to 2021 at Nakvak Brook ( $p < 0.05$ ) (Table 2; Supplemental Material A Tables S9 and S11). However, despite a lack of statistical significance, the relative frequency of selected summer and winter caribou forage in the control plots appears to be increasing with time at both sites and for both seasons (Table 2; Supplemental Material A Tables S7 and S8). Within the control and OTC plots, the relative frequency of avoided summer and winter forage declined significantly from 2009 to 2016 at Torr Bay ( $p < 0.001$ ;  $p < 0.01$ ; Table 2; Supplemental Material A Tables S7–S10), whereas at Nakvak Brook, the relative frequency of avoided summer forage and edible winter forage declined from 2010 to 2021 ( $p < 0.001$ ;  $p < 0.05$ ; Table 2; Supplemental Material A Tables S7–S10).

### Model selection

The results of model selection analysis are shown in Table 3.

### Caribou forage by rank

Analysis of point-frame data in relation to the three caribou forage ranks (selected, edible, and avoided) found that with time, avoided forage (both summer and winter) abundance declined at Torr Bay ( $t_{2016} = -0.83$ ;  $p < 0.001$  and  $t_{2016} = -0.24$ ;  $p < 0.01$ ; Fig. 3; see Supplemental Material A Tables S3–S6 for full model parameter estimates), with avoided winter forage abundance declining more in the OTC plots than in the control plots ( $t_{\text{OTC}^* \text{year}} = -0.32$ ;  $p < 0.01$ ). Selected winter forage abundance increased with time at Torr Bay ( $t_{2016} = 0.26$ ;  $p < 0.001$ ) and more so in the control plots than in the OTC



**Table 2.** Relative frequency of avoided, edible, and selected summer and winter forage in control and OTC plots at Torr Bay and Nakvak Brook, Labrador, comparing first (2009 and 2010) and last survey times (2016 and 2021) with odds ratios below each.

	Torr Bay				Nakvak Brook			
	Summer		Winter		Summer		Winter	
<b>CONTROL</b>								
<b>Rank</b>	<b>2009</b>	<b>2016</b>	<b>2009</b>	<b>2016</b>	<b>2010</b>	<b>2021</b>	<b>2010</b>	<b>2021</b>
Avoided	0.04	0.02	0.14	0.10	0.35	0.23	0.61	0.62
	0.43***		0.76**		0.48***		0.70	
Edible	0.32	0.28	0.65	0.65	0.07	0.12	0.29	0.24
	0.95		1.03		1.10		0.60*	
Selected	0.64	0.70	0.21	0.25	0.57	0.64	0.09	0.14
	1.16		1.24**		0.76		1.16	
<b>OTC</b>								
<b>Rank</b>	<b>2009</b>	<b>2016</b>	<b>2009</b>	<b>2016</b>	<b>2010</b>	<b>2021</b>	<b>2010</b>	<b>2021</b>
Avoided	0.06	0.02	0.14	0.08	0.34	0.20	0.63	0.66
	0.25***		0.55***		0.38***		0.72	
Edible	0.27	0.28	0.63	0.70	0.08	0.08	0.29	0.27
	0.96		0.98		0.72		0.69*	
Selected	0.67	0.70	0.23	0.22	0.58	0.72	0.08	0.07
	0.93		0.90		0.88		0.60*	

Note: Starred values show significant change in relative frequency with time (\*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; and \* $p < 0.05$ ). The degrees of freedom of each model here is 4. OTC, open-top chamber.

**Table 3.** Model parameters and distributions used in each statistical analysis. For Torr Bay and Nakvak Brook sites, forage rank models were explored ( $n = 6$ ; summer and winter models for 0, 1, and 2 forage ranks) while forage genera and lichen life models explored for the top six forage genera and lichen lifeforms ( $n = 7$ ; *Carex*, *Betula*, *Vaccinium*, *Salix*, *Cladonia*, *Stereocaulon*, and lichen lifeforms).

Analysis	Model type	Model equation	Distribution	Number of models
Torr Bay forage rank	GLMM	(Encounters $\sim$ TRTMT*YEAR + SUBSITE + (1 PLOT))	Negative Binomial	6
Nakvak Brook forage rank	GLMM	(Encounters $\sim$ TRTMT*YEAR + SUBSITE + (1 PLOT))	Negative Binomial	6
Torr Bay selected forage genera and lichen lifeforms	Zero-inflated GLMM	(Encounters $\sim$ TRTMT*YEAR + (1 PLOT))	Poisson	7
Nakvak Brook selected genera and lichen lifeforms	GLMM	(Encounters $\sim$ TRTMT*YEAR + SUBSITE + (1 PLOT))	Negative Binomial	7

Note: Further model details can be found in Supplemental Material A Tables S1–S2.

plots ( $t_{\text{OTC}^{\text{year}}} = -0.33$ ;  $p < 0.01$ ). At the Nakvak Brook site, avoided forage (both summer and winter) also declined in abundance with time ( $t_{2021} = -0.82$ ;  $p < 0.001$  and  $t_{2021} = -0.37$ ;  $p < 0.05$ ), but there were no significant changes in selected forage abundance.

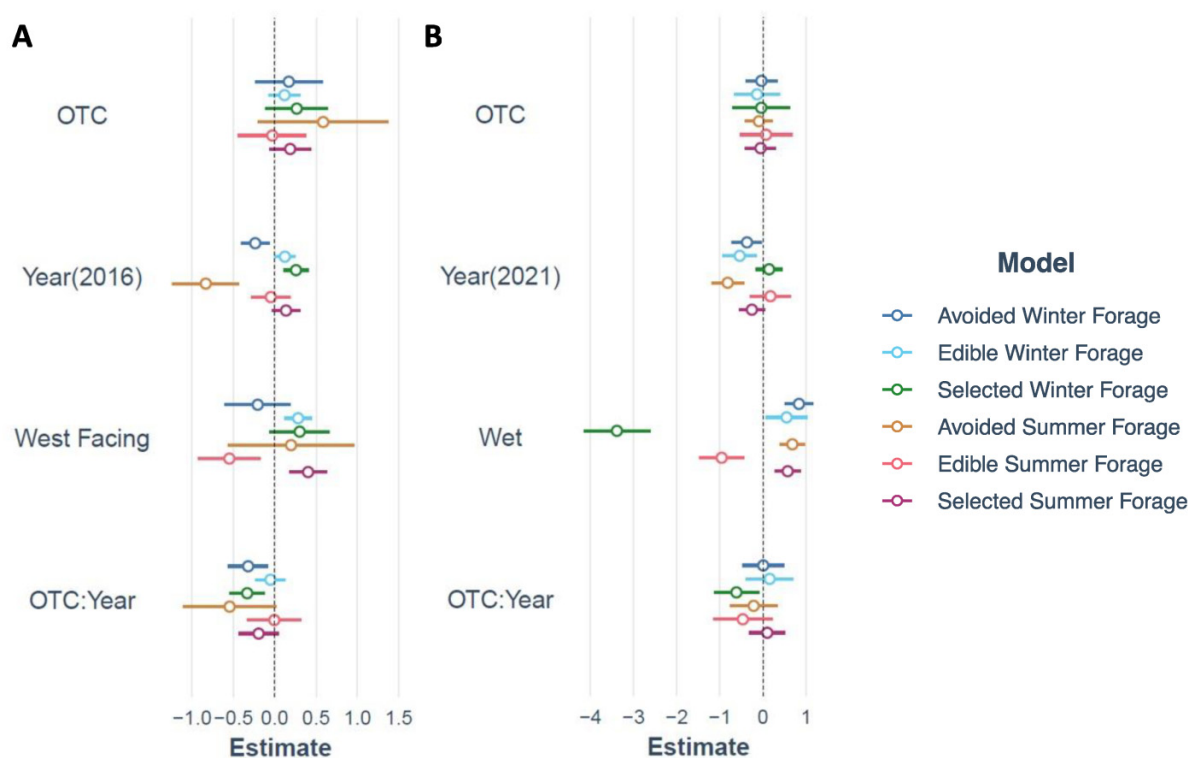
Subsite level factors (East facing/West facing, and Wet/Dry) were also found to have a significant effect on forage abundance. At Torr Bay, selected summer forage species were more abundant in the West facing plots ( $t_{\text{west}} = 0.40$ ;  $p < 0.001$ ; Fig. 3), while edible but not selected summer species were favored in the East facing plots ( $t_{\text{west}} = -0.55$ ;  $p < 0.01$ ), and edible but not selected winter species were favored in West facing plots ( $t_{\text{west}} = 0.28$ ;  $p < 0.001$ ). Moisture levels had a strong influence on forage abundance at Nakvak Brook. Avoided summer and winter forage along with selected summer

forage species were all more abundant in Wet than Dry plots ( $t_{\text{wet}} = 0.68$ ;  $p < 0.001$ ;  $t_{\text{wet}} = 0.83$ ;  $p < 0.001$ ;  $t_{\text{wet}} = 0.57$ ;  $p < 0.001$ ) while, selected winter forage was significantly more abundant in Dry plots rather than Wet plots ( $t_{\text{wet}} = -3.39$ ;  $p < 0.001$ ).

### Caribou forage by genera

To better understand changes in selected forage with time, we analyzed six selected forage genera (*Carex*, *Betula*, *Vaccinium*, *Salix*, *Cladonia*, and *Stereocaulon*) of the 11 selected caribou forage genera since five of the genera (*Alectoria*, *Cetraria*, *Equisetum*, *Flavocetraria*, and *Gowardia*) had insufficient observations to parameterize GLMMs ( $X < 250$  cumulative occurrences for both sites). Our genera level zero-inflated Poisson GLMMs for the Torr Bay site showed increased abundances

**Fig. 3.** A generalized linear mixed model (GLMM) showing the effects of OTC treatment, year, subsite, and year\*treatment interactions on the abundance of avoided, edible, and selected summer and winter forage types at Torr Bay (A) and Nakvak Brook (B). Control plots, the 2010 (A) and 2009 (B) surveys, and Dry and East facing plots are the baseline categories that the effects are measured against. Significant effects have 95% confidence interval bars that do not overlap with zero. Note that the range of values along the x-axes differ between plots A and B.



of both *Betula* and *Vaccinium* species with time ( $z_{2016} = 0.35$ ;  $p < 0.001$ ;  $z_{2016} = 0.19$ ;  $p < 0.001$ ; Fig. 4). *Betula* experienced a greater increase in OTC plots while *Vaccinium* experienced a greater increase in control plots ( $z_{\text{OTC} \times \text{time}} = 0.28$ ;  $p < 0.01$ ;  $z_{\text{OTC} \times \text{time}} = -0.21$ ;  $p < 0.001$ ). There were no significant changes in abundance with time for *Carex*, *Salix*, *Cladonia*, *Stereocaulon*, and “lichen”.

At the Nakvak Brook site we applied a nonzero-inflated negative binomial GLMM. We found that *Salix* species declined in abundance from 2010 to 2021 ( $b_{2021} = -0.28$ ;  $p < 0.001$ ; Fig. 4). This change in abundance appears to be driven by a decline in *S. herbacea* over time. No significant changes in abundance with time were found for the other five forage genera, nor pooled lichen species. Plot moisture class (Wet/Dry) played a significant role in genera abundance. *Carex* was more abundant in Wet plots than Dry plots ( $b_{\text{wet}} = 2.13$ ;  $p < 0.001$ ), while *Cladonia*, *Stereocaulon*, and lichens are more abundant in Dry plots ( $b_{\text{wet}} = -3.42$ ;  $p < 0.001$ ;  $b_{\text{wet}} = -4.49$ ;  $p < 0.001$ ;  $b_{\text{wet}} = -3.66$ ;  $p < 0.001$ ).

## Discussion

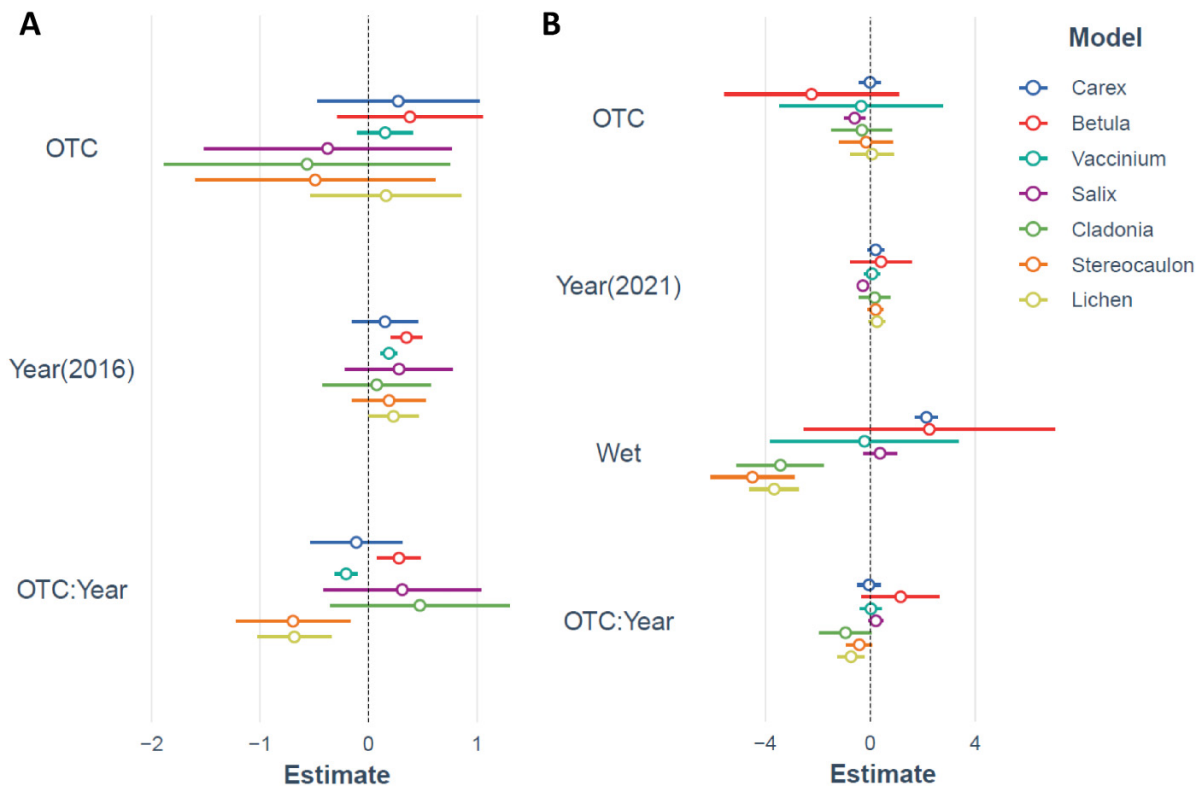
Our study found that the relative frequency of selected winter caribou forage was far lower than the relative frequency of selected summer forage at both Torr Bay and Nakvak Brook. The study’s control plots, which are repre-

sentative of the greater landscape, comprised 70% selected summer forage, and only 25% selected winter forage during the most recent Torr Bay survey (2016). Similarly, in the most recent control plot surveys at Nakvak Brook (2021), 64% of the total vegetation was selected summer forage and only 14% was selected winter forage (Table 2). Whereas control plots at neither site showed significant changes in the relative frequency of selected winter forage with time, we did see a significant decline in selected forage abundance in the Nakvak Brook OTC plots (Table 2) indicating how future warming could influence the availability of winter forage. At our two study sites, at which caribou grazing pressure is low, our findings suggest that selected summer forage is more available than selected winter forage, with the possibility of some areas likely to experience even less winter forage availability as warming continues.

Other studies also found caribou to be more forage limited during the winter; however, these studies found forage limitations were a result of small winter ranges, or limited suitable forage sites resulting in greater caribou concentration and over grazing of lichens (Bergerud 1963; Heggberget et al. 2002). Moreover, the availability of highly-selected winter forage is expected to decline with climate change (Alatalo et al. 2017; Chagnon and Boudreau 2019). As growing conditions become increasingly favorable for shrubs, they will continue to expand across the tundra and outcompete lichens (Myers-Smith et al. 2011; Elmendorf et



**Fig. 4.** A generalized linear mixed model (GLMM) showing the effects of OTC treatment, year, subsite, and year\*<sup>treatment</sup> interactions on the abundance of six genera of selected caribou forage and lichen lifeforms at Torr Bay (A) and Nakvak Brook (B). Control plots, the 2010 (A) and 2009 (B) surveys, and Dry and East facing plots are the baseline categories that the effects are measured against. Significant effects have 95% confidence interval bars that do not overlap with zero.



al. 2012). Limited winter forage availability could have serious implications for caribou since winter is when caribou face the highest thermoregulation costs and demands for fetal growth (Parker et al. 2005). Furthermore, winter forage limitations could influence caribou movement patterns. Schmelzer and Otto (2003) found evidence of range drift in the GRC herd, when an area was overgrazed in a previous year, caribou shifted their migratory patterns to avoid those areas the subsequent year. The TMC are a non-migratory mountain caribou population, they do however display elevational movement patterns to escape predators and poor forage conditions (Couturier et al. 2010, 2015). Inuit Knowledge says that when caribou food runs out, the caribou will move to find other food (Wilson et al. 2014) and, therefore, winter forage limitations could cause changes in TMC movements.

At Torr Bay, we found increases in abundance of *Betula* and *Vaccinium* species with ambient warming over the duration of our study period (Fig. 4). This result supports our hypothesis that we would see increased shrub abundances consistent with shrubification. Other long-term studies from Quebec and Alaska also found similar patterns (Sturm et al. 2001; Ropars and Boudreau 2012). Inuit Knowledge also notes a recent increase in shrub abundance in the Torngat Mountains (Wilson et al. 2014; Cuerrier et al. 2015; Siegwart Collier 2020). However, at a global scale, recent syntheses document vegetation responses to climate change are not

uniform across the Arctic (Myers-Smith et al. 2011; Elmendorf et al. 2012; Myers-Smith et al. 2020).

A global synthesis of two decades of ecological monitoring (ITEX) found that shrubs exhibited the greatest rate of expansion in warm tundra regions particularly in moist to wet areas while cold regions were more resistant to shrub expansion (Elmendorf et al. 2012; Henry et al. 2022). The Circumpolar Arctic Vegetation Map (Walker et al. 2005) classifies Northern Labrador as part of bioclimate subzone E, which is the warmest of the 5 Arctic subzones, categorized by mean summer temperatures of 10–12 °C, taller shrubs, 80%–100% vascular plant cover, and a closed canopy (Walker et al. 2005). It is in subzones D and E that Elmendorf et al. (2012) expect future climate-induced shrub expansion to be the greatest. This is supported by our finding that *Betula* and *Vaccinium* species have increased in abundance over time. Contrarily, we found that *Salix* species declined in abundance over the 11 years at the Nakvak Brook site (Fig. 4). One possible explanation for this finding is that in recent years, we have observed visible drying of wet areas at the Nakvak Brook site (Davis et al. 2021a). This drying trend could be negatively impacting *Salix* expansion since willow species tend to grow in moist environments (Boulanger et al. 2014). Furthermore, our results showed that avoided summer forage declined at both sites over time. This decline appears to be driven by reductions in moss abundance at both sites. At Torr Bay moss declines were primarily experienced by *Polytrichum* and *Aulacomium* while

*Sphagnum*, *Aulocomm*, *Dicranum*, *Pogonatum*, *Drepanocladus* all decreased drastically at Nakvak Brook (see Fig. S3 in Supplemental Material A). Similar to *Salix*, declines in moss species may be driven by drying of wet sites (Elmendorf et al. 2012), but could also have been affected by the encroachment of shrubs, especially at the Torr Bay site where birch and ericaceous species increased in abundance.

Similar to findings of Elmendorf et al. (2012), Davis et al. (2021b), and Myers-Smith et al. (2015), our results showed that vegetation abundance was strongly influenced by soil moisture availability. The plots at Nakvak Brook were split between wet and dry areas. We found that selected winter forage was significantly more abundant in Dry plots while selected summer forage was far more abundant in Wet plots. The greater abundance of selected winter forage in Dry plots can be explained by our findings that *Cladonia*, *Stereocaulon*, and the lichen functional group were significantly more abundant in Dry plots. Additionally, we found that *Carex* was far more abundant in Wet plots which could partially explain the greater abundance of selected summer forage in those plots.

Tundra areas with higher soil moisture have been found to exhibit greater climate sensitivity to warming thus experiencing greater shrub expansion (Elmendorf et al. 2012; Myers-Smith et al. 2015; Loranty et al. 2018; Davis et al. 2021b). A remote sensing study of Torngat Mountains National Park by Davis et al. (2021b) found that 28.8% of raster pixels classified as wet vegetation in 1985/89 transition to shrub vegetation pixels by 2015/19, whereas only 1.4% and 3% of dry and non-vegetated pixels underwent a similar transition. Furthermore, decreased soil moisture from experimental warming coincided with community turnover from sedge and grass dominated meadow to birch and ericoid dominated heath communities (Scharn et al. 2021). Climate change is expected to impact moisture availability across the Arctic as permafrost thaws and snow melt occurs earlier in the year (Scharn et al. 2021). In northern Labrador, the maximum precipitation is predicted to increase across the region over the next 30 years (Climate Atlas of Canada 2019), but there is uncertainty given the considerable variability across future projections (Barrette et al. 2020). Notably, Davis et al. (2021b) found that the total amount of wet vegetation in Torngat Mountains National Park increased over time with most gains coming from the dry vegetation class. It is clear from climate forecasts (Climate Atlas of Canada 2019) and our own soil moisture data (see Davis et al. 2021a) that soil moisture in Northern Labrador will be impacted by climate change, and a greater relative frequency of shrub and wet vegetation cover is expected in the region. Moreover, we would expect this to increase the availability of summer caribou forage while decreasing the availability of winter forage as the region continues to experience warming.

A surprising result from our study was that neither experimental warming nor ambient warming (time factor in models) had any significant effects on *Cladonia*, *Stereocaulon*, nor the “lichen” functional group at either site. Based on results of previous studies (Elmendorf et al. 2012; Alatalo et al. 2017; Chagnon and Boudreau 2019), we expected that lichens would have declined with time and warming as a result of

greater competition with shrubs. We have two potential explanations for this finding: (1) Dry sites, where lichen are dominant, may need to transition to wet sites before shrub growth becomes a significant driver (Davis et al. 2021a). (2) A lack of change in lichen abundance could be explained by the presence of an opposing signal to climate change. A recent study by Andruko et al. (2020) looked at decadal growth rates of dwarf birch in the low arctic and found that across multiple habitat types dwarf birch growth was enhanced. However, since warming trends were found to be limited at these sites, Andruko et al. (2020) suggested that increased birch growth could be explained by reduced browsing from recent caribou herd declines. Our study region, the Torngat Mountains, also recently experienced a release from browsing pressure. In the early 1990's, the GRC herd was comprised of 770 000 individuals (Couturier et al. 1996) but, by 2018 this number dropped to around 5500 individuals (Government of Newfoundland and Labrador 2018), though has increased to 7200 in 2022 (Government of Newfoundland and Labrador 2022). This decline has resulted in a contraction of the GRC range away from the Torngat Mountains (Bergerud et al. 2007), potentially reducing landscape browsing pressure. With reduced GRC browsing, we would expect to see highly-selected forage species such as lichens rebounding. This could create opposing signals; climate change negatively impacts lichen abundance while reduced browsing benefits their growth. Reduced browsing could have also had an effect on shrub growth; however, lichens are very slow growing and unlike shrubs do not experience compensatory growth so we would expect this signal to be stronger for lichens (Pegau 1968; Champagne et al. 2012). Given these limitations we cannot reliably disentangle climate change and reduced grazing signals, but this is a potential avenue for future research.

It is evident that over the past several decades, shrub abundance has been increasing across the Arctic (Sturm et al. 2001; Fraser et al. 2011; Elmendorf et al. 2012; Bjorkman et al. 2018). This rapid shrub expansion resulting from Arctic warming has been shown to negatively impact lichens, a key winter forage species for caribou (Fraser et al. 2014; Alatalo et al. 2017; Chagnon and Boudreau 2019). On the other hand, availability of selected summer caribou forage such as *Betula glandulosa* and *Vaccinium uliginosum* is increasing. Warming has been found to reduce the nutritional value and digestibility of caribou forage shrubs by decreasing nitrogen content and increasing phenolics in plant tissues (Turunen et al. 2009; Zamin et al. 2017). Furthermore, a study by Vowles et al. (2017) found that non-palatable evergreen shrubs are spreading faster than palatable deciduous shrubs since deciduous shrub expansion is inhibited by caribou browsing. This result would suggest that climate induced shrub expansion is not only limiting winter forage availability, but with time could limit summer forage if non-palatable evergreen shrubs increase in abundance. From our point-frame dataset, we found that at both Torr Bay and Nakvak Brook there was a significant increase in the relative frequency of evergreen *Rhododendron* spp. We also found that at Nakvak Brook, the only site where *Harrimanella hypnoides* L. was present, it increased in relative frequency, while *Empetrum nigrum*, only present at Torr Bay, showed no change in the relative

frequency (see Table S11 and Figs. S1–S2 in Supplemental Material A).

Not only has Arctic warming been shown to influence the availability of caribou forage, but it is also impacting caribou in several other ways. Climate change is expected to cause a “trophic mismatch” where the timing of calving misaligns with forage availability (Post and Forchhammer 2008). Furthermore, climate change is causing later freezing and earlier breakup of ice on lakes and rivers (Magnuson et al. 2000), which has had consequences for caribou migration patterns (Côté et al. 2012). Climate change is predicted to cause an 89% decline in suitable caribou habitat in North America over the next 60 years (Yannic et al. 2014). In Labrador and Quebec, spring and summer ranges suitable for the GRC are predicted to shrink to just the northeastern section of the Quebec–Labrador Peninsula over the next 30–50 years (Sharma et al. 2009). Without stronger policies and international action to reduce greenhouse gas emissions, climate change will continue to change the Arctic threatening caribou survival. A loss of caribou would have immense consequences for Inuit well-being as caribou are a cultural keystone species.

## Conclusion

Understanding caribou forage availability is necessary for the long-term conservation of caribou in Northern Labrador. Our study found that the relative frequency of total vegetation suitable for caribou was far higher in the summer months than during the winter months at both study sites. This result suggests that selected caribou forage is more available in the summer than during the winter. Dry, lichenous, and windblown areas optimal for winter foraging should be prioritized for conservation. We found an increase in selected winter forage abundance from 2009 to 2016 at Torr Bay and declines in avoided summer forage at both sites over time. In general, we did not find that experimental warming had a greater effect on vegetation abundance than ambient warming (time factor). Our results showed that birch and ericaceous forage species increased over time, while lichen species were not significantly affected. Understanding how specific forage species are expected to change with warming will help to predict how caribou may become forage limited in the future, especially if population sizes begin to rebound. Taken together, this knowledge could be useful for ecosystem managers where change occurring in tundra habitats can be viewed through a caribou forage lens, with the potential for identifying and conserving areas of highly-selected summer and winter forage. These conservation and management measures may have profound impacts on TMC and contribute to the social-ecological resilience of northern communities. While results of this study are specific to the species assemblages found in TMNP, this approach could be applied to other long-term tundra vegetation datasets (e.g., ITEX) to assess caribou forage abundance in different regions.

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### Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request. Data are co-owned by the Nunatsiavut Government.

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## Competing interests

The authors declare there are no competing interests.

## Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/as-2023-0047>.

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