Remotely sensed trends in vegetation productivity and phenology during population decline of the Bathurst caribou (*Rangifer tarandus groenlandicus*) herd

Katherine D. Dearborn and Ryan K. Danby

Abstract: The Bathurst caribou (*Rangifer tarandus groenlandicus* (Borowski, 1780)) herd declined from ~349 000 animals in 1996 to ~8200 in 2018. Climate-driven changes to tundra and boreal vegetation is one hypothesis for the decline. We modelled and mapped annual productivity and phenology across the herd's range using enhanced vegetation index (EVI) data derived from a Moderate Resolution Imaging Spectroradiometer (MODIS) time series spanning 2000–2017. Maximum annual EVI, growing season length, and time-integrated EVI increased significantly on 16%, 18%, and 49% of the core annual range, respectively. Trends toward longer growing seasons were driven entirely by earlier spring green-up and, along with time-integrated EVI, were most prevalent in tundra regions. Trends in forested regions were overwhelmingly related to the influence of forest fires, which burned more than half of the range below the forest–tundra ecotone since 1965. These trends suggest that climate-driven changes in production and phenology have occurred in the tundra and forest–tundra portions of the range and could have contributed to the recent herd decline. However, the trends may also be a result of herd decline itself, given the loss of this large herbivore from the landscape. Elucidating cause and effect will require comprehensive analysis of interactions between climatic variables, herd dynamics, and vegetation change, complemented by targeted field investigations.

Key words: remote sensing, vegetation index, NDVI, EVI, MODIS, caribou, Northwest Territories, Nunavut, Arctic greening, boreal browning.

Résumé : La harde de caribous (*Rangifer tarandus groenlandicus* (Borowski, 1780)) de Bathurst est passée de ~349 000 animaux en 1996 à ~8200 en 2018. Les changements dans la végétation de la toundra et de la forêt boréale induits par le climat sont une des hypothèses de ce déclin. Les auteurs ont modélisé et cartographié la productivité annuelle et la phénologie sur l'ensemble de l'aire de répartition de la harde à l'aide de données d'indice de végétation amélioré (EVI) dérivées d'une série chronologique MODIS (spectroradiomètre imageur à résolution moyenne) couvrant la période 2000–2017. L'EVI annuel maximum, la durée de la saison de croissance et l'EVI intégré dans le temps ont augmenté de manière significative sur 16, 18 et 49 % de l'aire de répartition annuelle principale, respectivement. Les tendances à l'allongement de la saison de croissance étaient entièrement dues à un verdissement printanier plus précoce et, parallèlement à l'EVI intégré dans le temps, étaient les plus répandues dans

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les régions de toundra. Les tendances dans les régions forestières étaient essentiellement liées à l'influence des feux de forêt qui ont consommé plus de la moitié de l'aire de répartition sous l'écotone forêt-toundra depuis 1965. Ces tendances suggèrent que des changements dans la production et la phénologie déterminés par le climat se sont produits dans les portions de toundra et de forêt-toundra de l'aire de répartition et pourraient avoir contribué au récent déclin de la harde. Cependant, les tendances peuvent également être le résultat du déclin de la harde elle-même, étant donné la perte de ce grand herbivore dans le paysage. L'élucidation des causes et des effets nécessitera une analyse exhaustive des interactions entre les variables climatiques, la dynamique des hardes et les changements de la végétation, complétée par des enquêtes de terrain ciblées. [Traduit par la Rédaction]

Mots-clés : télédétection, indice de végétation, NDVI, EVI, MODIS, caribou, Territoires du Nord-Ouest, Nunavut, verdissement arctique, brunissement boréal.

Introduction

The direct and indirect effects of recent climate warming have altered the structure and composition of vegetation in northern regions (Price et al. 2013). Several different methods have been used to quantify this change, each with their own advantages and shortcomings relative to each other (Danby 2011). Field-based methods, such as repeat surveys and dendrochronology, can identify specific types and mechanisms of change, but are restricted to small geographic areas. In contrast, satellite remote sensing can characterize change in vegetation productivity over broad spatial extents at regular time intervals, making it well suited for quantifying change across large, remote regions. Vegetation indices derived from satellite imagery have been used extensively for Arctic and subarctic vegetation monitoring. The most common of these is the normalized difference vegetation index (NDVI), which is effective for differentiating productive and unproductive vegetation by using measurements of near-infrared and red reflectance (Goetz et al. 2005; Bhatt et al. 2010; Reynolds et al. 2012). The enhanced vegetation index (EVI) is calculated similarly, but includes several coefficients that adjust for the influence of bare soil and aerosol scattering (Huete et al. 2002).

Several satellite sensors have been used for monitoring northern vegetation, each of which cover different time periods and have different temporal and spatial resolutions. The Advanced Very High Resolution Radiometer (AVHRR) and Landsat-based sensors have been collecting red and near-infrared reflectance data since the 1980s. AVHRR has a high temporal resolution (revisit times of less than 24 h), which is necessary for the detection of phenological change, but very coarse spatial resolution (1–8 km pixels depending on the data set). Landsat sensors, in contrast, have high spatial resolution (30 m pixels), but poor temporal resolution (16-day revisit time), which greatly limits their ability to detect phenological events (White et al. 2014). The Moderate Resolution Imaging Spectroradiometer (MODIS) has been in operation since 2000 and combines high temporal resolution (daily revisit times) with moderate spatial resolution (250 m pixels). These characteristics make it possible to quantify trends in vegetation phenology as well as productivity at a spatial resolution that is suitable for regional- and landscape-scale research questions (Zhang et al. 2004; Ganguly et al. 2010).

Although different satellite data sets can yield different results (see Guay et al. 2014), most studies have shown that tundra landscapes have undergone an increase in productivity over the past several decades, termed “greening”, while boreal forests have sometimes undergone a decrease, termed “browning” (Ju and Masek 2016; Wang and Friedl 2019). Tundra greening is often attributed to a warming-induced increase in the abundance or growth of tall deciduous shrubs (e.g., Forbes et al. 2010; Berner et al. 2020), while boreal browning has been attributed to heat-induced drought stress in conifers and (or)

increased forest disturbance due to fires and insect infestation (Sulla-Menashe et al. 2018; Boyd et al. 2019). Concurrently, the length of the growing season has generally increased in northern regions over the past several decades (Goetz et al. 2005; Zhu et al. 2012). Notably, however, these productivity and phenology trends are spatially variable at landscape scales (Raynolds et al. 2013; Fraser et al. 2014; Myers-Smith et al. 2020), and trends within specific regions or time periods can directly contradict broader-scale findings (e.g., Park et al. 2016; Wang and Friedl 2019).

These recent changes in vegetation productivity and phenology are likely altering wildlife habitat suitability for a number of species that occupy boreal and tundra regions (e.g., Tape et al. 2016; Wheeler et al. 2018). One species of particular concern is barren-ground caribou (*Rangifer tarandus groenlandicus* (Borowski, 1780)) (Bradshaw et al. 1995; Price et al. 2013). Caribou have immense socioeconomic value to northern communities (Kendrick et al. 2005) and play an important ecological role in northern ecosystems; in part through the impact of grazing on plant communities, and in part by sustaining predator populations (Musiani et al. 2007; Bernes et al. 2015). Several herds of barren-ground caribou have declined substantially over the past few decades (Vors and Boyce 2009). The cause of these declines is not well understood, as populations are influenced by a variety of factors that can lead to increased mortality such as disease, hunting, predation, and catastrophic weather events (Festa-Bianchet et al. 2011). Because they are a migratory species with an annual range that spans both tundra and boreal forest ecosystems, factors related to changes in habitat quality could also be associated with their decline. These include changes in forest fire regimes; impacts of human activities such as mining, forestry, and road construction; and climate-related changes in vegetation and snow cover (Festa-Bianchet et al. 2011). Specific links amongst these habitat changes and the direct causes of mortality are difficult to quantify due in part to the vast spatial extent of their habitat as well as the interactive and potentially cumulative effects associated with them (Gunn et al. 2011).

The extent to which climate-driven shifts in vegetation productivity and phenology are affecting habitat quality of barren-ground caribou remains unclear, but there is emerging evidence that vegetation change could be linked to population declines (Fauchald et al. 2017; Rickbeil et al. 2018). Like other large herbivores, barren-ground caribou are highly reliant on forage quality and availability. Thus, they could be affected in numerous ways by both greening and browning trends, as well as changes in phenology. For example, if green-up is occurring earlier on their late-spring tundra range, it could increase the availability of forage to cows prior to calving (Cebrian et al. 2008). Paradoxically, however, an increase in tundra productivity due to the proliferation of tall deciduous shrubs could be detrimental to caribou. Encroachment of shrubs has been linked to a reduction in the abundance of cottongrass (*Eriophorum* spp.), an important forage species for calves and nursing cows (Cebrian et al. 2008; Fraser et al. 2014) and American dwarf birch (*Betula glandulosa* Michx.) — a species closely associated with Arctic greening in North America — is less preferred as browse than other species due to its production of phenolic compounds (Christie et al. 2015). Lastly, recent climate-driven increases in fire severity and frequency could be negatively impacting caribou because fire reduces the abundance of lichen, an important food source for barren-ground caribou on their winter range (Jandt et al. 2008; Joly et al. 2010; Lewis et al. 2019).

Given the spatial variability in climate-related vegetation change observed throughout the circumpolar north, broadscale trends in productivity and phenology are not particularly useful for understanding potential links between vegetation change and the population dynamics of specific herds. Rather, it is necessary to quantify the specific magnitude and extent of vegetation change within each seasonal component of a herd's range prior to investigating these links. Understanding changes in phenology is equally important as

an understanding of productivity. For this study, we used MODIS imagery to quantify vegetation change on the range of the Bathurst barren-ground caribou herd from 2000 to 2017. The herd is of considerable conservation concern at present because it declined from approximately 350 000 animals in 1996 to fewer than 10 000 in 2018 (GNWT 2019). Specifically, we asked the following questions:

1. How did vegetation productivity and phenology change across the range of the Bathurst herd during their recent period of population decline?
2. How did the direction and magnitude of this change vary among the different seasonal components of the herd's range and between tundra and forest components of the range?

We did not set out to explicitly test the role of vegetation change as a contributing factor in the Bathurst herd's decline. However, there are several ongoing investigations into the causes of caribou herd declines in northern Canada and Alaska, including the Bathurst herd. The results of this study should be useful in providing the data necessary to test the relationships between landscape-scale vegetation change and caribou population dynamics.

Methods

Study region

The range of the Bathurst caribou herd spans the traditional homelands of both Dene and Inuit peoples, and the herd has been an important source of sustenance and cultural value for generations (Parlee and Caine 2018). The herd traditionally migrates between its calving range near Bathurst Inlet on the Arctic Ocean in the Kitikmeot Region of Nunavut and its winter range in the boreal forests of central Northwest Territories and as far south as northern Saskatchewan. The tundra portion of the herd's range is located entirely within the Southern Arctic ecozone. The forested portion of the herd's range falls largely within the Taiga Shield ecozone, although western portions extend onto the Taiga Plains ecozone. Fire is a prominent landscape process in both of the Taiga ecozones and plays a dominant role in governing forest structure and composition. Describing a fire regime for the region is challenging as fire size and frequency vary considerably and fire events are often of mixed severity (Lewis et al. 2019). Nonetheless, over 50% of the treed area contained within the range of the Bathurst herd has burned at least once since fire mapping began in 1965 (Table 1).

In 2019, the Government of Northwest Territories released the Bathurst Caribou Range Plan (GNWT 2019). The area covered by the plan is roughly triangular in shape and covers over 320 000 km² of Northwest Territories, Nunavut, and northern Saskatchewan. The planning area was based on Traditional Indigenous Knowledge of the herd's range as well as location data derived from radio-collared female caribou from 1996 to 2014. The plan's purpose is to provide guidance in the process of land-use decision-making, and it outlines an adaptive management framework for managing cumulative impacts on Bathurst caribou. Within this framework, the plan identifies several priority indicators for environmental monitoring, including vegetation change (GNWT 2019).

Data acquisition

There are several MODIS-derived data sets that are freely available to users in North America. These include the data sets developed by the United States Geologic Survey, the Canadian Centre for Remote Sensing, and NASA. They each differ in terms of the MODIS "Collection" they are derived from (i.e., the set of corrections and pre-processing algorithms applied to the raw imagery by NASA), as well as the compositing method used. Compositing is the process of selecting a single high-quality pixel from a given time period to represent

Table 1. The total land area, burned area (i.e., area affected by fire since 1965), and unburned area within each of the core seasonal components of the range of the Bathurst herd (core use range), and each of the components of the range planning area (extended range).

		Total land area (km ²)	Burned area (km ²)	Unburned area (km ²)
Core use range	Annual	98 310	12 336	85 974
	Spring	9926	20	9906
	Calving	14 126	0	14 126
	Summer	64 815	44	64 771
	Fall	43 009	4972	38 037
	Winter	45 473	19 697	25 776
Extended range	Range planning area	320 692	88 103	232 589
	Above treeline	107 316	41	107 275
	Forest line to treeline	75 316	10 609	64 707
	Below forest line	138 060	77 453	60 607

Note: Values are land area only; all areas classified as water from Moderate Resolution Imaging Spectroradiometer data were removed from the data tabulations.

that period and is primarily done to eliminate cloud-covered pixels. As the MODIS sensor has an approximate revisit time of 1 day, relatively short composite periods are possible (7–16 days). The United States Geologic Survey data set (eMODIS) has the shortest composite period (7 days) but is not available for northern Canada. The Canadian Centre for Remote Sensing data set has a 10-day composite period and has less geometric distortion over northern Canada than the NASA data set (Ji et al. 2010). However, it was developed using Collection 5 MODIS data, which has known issues with sensor degradation that have since been corrected for in Collection 6 (Wang et al. 2012; Zhang et al. 2017).

We therefore opted to use NASA's Collection 6 data, which are provided in 16-day composites at 250 m resolution (Product #: MOD13Q). Although this composite period is longer than that of other MODIS products, we considered it to be the most conservative option because longer composite periods have a lower proportion of poor-quality pixels (Ji et al. 2010; Verbyla 2015). NASA offers both NDVI and EVI products. We chose to use EVI data because they have shown to be more sensitive to phenological change (Xiao et al. 2005; Peng et al. 2017) and because minimizing the influence of bare soil backscatter can be important in tundra landscapes (Huete et al. 2002). These data are available from February 2000 to present, and are divided into "tiles", each of which cover an area approximately 10° in latitude by 10° in longitude. As images are provided in 16-day composites, Collection 6 products consist of 23 images per year, or 406 images in total from February 2000 to October 2017 (when we initiated the study).

To ensure coverage of the entire range of the Bathurst caribou herd, we downloaded all available years of 16-day composite EVI data from three MODIS tiles (406 composite periods × 3 tiles = 1218 files). Composite images still contain poor-quality pixels, so we obtained the accompanying pixel quality data provided by NASA as well. We then used the MODIS Reprojection Tool provided by NASA to mosaic the three EVI and pixel quality images together for each composite period. We reprojected the mosaicked images from their original global Sinusoidal projection to the Lambert Conformal Conic projection used by the Government of the Northwest Territories.

Data processing and analysis

Time series of vegetation indices are frequently noisy due to differences in view angle, illumination patterns, aerosol content in the atmosphere, and cloud cover between composite periods. This can make derivation of phenological metrics challenging.

Fig. 1. Illustrative example of curve-fitting and derivation of productivity and phenology metrics for a single pixel. Open black circles represent EVI values extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS) composite data. The red curve represents values modelled using a double logistic function. The size of the open black circles is indicative of the quality of the MODIS data; high-quality data was weighted 1.0 in modelling, moderate-quality data was weighted 0.5, and low-quality data was weighted 0.1. Letters indicate the values of the phenological metrics derived from the modelled data and used in the multiannual trend analysis.

One solution is to remove poor-quality pixels and fill in missing values via interpolation of the surrounding pixels (Zhang et al. 2004; Miles and Esau 2016). The other option is to minimize noise by fitting a curve to measured EVI values (Cai et al. 2017). We chose the latter option, as it retains more data. We fit a double logistic function to measured values, as it performs better than other functions when there are no ground-based phenology calibration data available (Beck et al. 2006; Cai et al. 2017). We reduced the influence of poor-quality pixels on fitted curves by weighting them in accordance with the pixel quality information provided by NASA. Specifically, we assigned weights of 1.0, 0.5, and 0.1 to good-quality, medium-quality, and low-quality pixels, respectively. Curve fitting was carried out in Timesat (version 3.3) (Jönsson and Eklundh 2004).

We then used modelled EVI values to extract annual productivity and phenology metrics for each pixel (Fig. 1). We derived maximum annual EVI, start and end of season dates, season length (the difference in days between end and start of season dates), and time-integrated EVI (area under the modelled EVI curve). Previous studies have calculated green-up and senescence dates by identifying the days on which vegetation indices surpassed or fell below a user-defined threshold value (Høgda et al. 2013; Tan et al. 2013; Kobayashi et al. 2016), or by identifying “inflection points” when the rate of increase or decrease in vegetation index values was greatest (Zhang et al. 2003; Beck et al. 2006). The latter is generally more sensitive to snowmelt than green-up in the spring, and can be overly influenced by late season drought stress (Jin et al. 2017; Shang et al. 2017). Thus, we opted to use a threshold-based approach. Specifically, we identified the days when modelled EVI values rose above and fell below a threshold of 0.72 of the amplitude of the annual curve as the start and end of season dates, respectively (Cai et al. 2017).

Next, we performed pixel-wise linear regressions to determine the direction and magnitude of trends in productivity and phenology metrics between 2000 and 2017 ($n = 18$ years for each pixel), as well as the statistical significance of these trends. We then used ArcGIS (version 10.5) to calculate percentages of significant positive and negative trends in core areas of each seasonal component of the herd's range. The five seasonal ranges were identified by the Government of the Northwest Territories using GPS telemetry data obtained between 1996 and 2015 (GNWT 2019). Core use areas were derived using kernel density analyses of the collar data and defined using a relative frequency of occurrence of 95% (i.e., 95% utilization distributions). The seasonal ranges we used were "spring migration" (20 April to 1 June), "calving grounds" (2 June to 28 June), "summer range" (29 June to 6 September), "fall/breeding range" (7 September to 30 November), and "winter range" (1 December to 19 April) (Fig. 2). We also calculated percentages of significant trends within the total core annual range and the broader "range planning area" of the herd, which includes areas that have historically supported the herd. We segmented the range planning area into areas north of treeline, between treeline and forest line (the forest–tundra ecotone), and south of forest line (Timoney et al. 1992; Timoney and Mamet 2020). We masked out all waterbodies using the MODIS land–water mask generated by NASA so that percentages of trends in each range component reflect the total terrestrial area, rather than total surface area.

Fire has a significant effect on satellite-derived vegetation indices in boreal regions, with recently burned areas frequently expressing browning trends and older burns expressing greening trends (Bonney et al. 2018). However, vegetation indices in boreal regions have been shown to return to pre-fire values approximately 50 years following fire (Goetz et al. 2007; Tan et al. 2013). In an attempt to isolate trends not associated with fire (and, therefore, reflect trends due solely to climate variability and change), we determined trends separately for areas that have burned and areas that have not burned since 1965 (Table 1). The Canadian National Fire Database was used to delineate these areas (Natural Resources Canada 2017).

Results

The range of the Bathurst caribou herd experienced significant changes in vegetation productivity and phenology from 2000 to 2017. However, these changes were spatially variable. Here we report trends of each metric for the core annual range and its seasonal components (depicted in Figs. 3–5, summarized in Fig. 6), as well as for the entire range planning area and its tundra, forest–tundra ecotone, and forest regions (depicted in Figs. 3–5, summarized in Fig. 7). Only statistically significant trends ($p \leq 0.05$) are reported. In summarizing the amount of change in each of these regions, we report both the total amount of significant change (i.e., when burned areas are included), as well as the amount of significant change when burned areas are excluded.

Productivity, as measured by seasonal maximum EVI values, increased on 16% of the core annual range, or 16 191 km². This dropped to 13% (12 941 km²) when burned areas were excluded from calculations. These positive trends were more or less evenly distributed throughout the various seasonal ranges, although they were most common in the fall range, which spans the tundra and forest–tundra ecotone. Negative trends in vegetation productivity were much less common, occurring in only 3% of the core annual range (3191 km²) when burned areas were included and 1% (839 km²) when burned areas were excluded (Figs. 6 and 7). Trends in productivity in wooded portions of the range below treeline were highly variable and contingent on fire history. Areas that burned during the study period exhibited strong negative trends in maximum EVI while areas that had burned in the 20 years prior exhibited strong positive trends (Fig. 3).

Fig. 2. Seasonal ranges of the Bathurst caribou herd based on 95% utilization distributions (95UD) derived from GPS collar data obtained between 1996 and 2015 by the Government of the Northwest Territories. “Spring” includes movements from 20 April to 1 June (A), “Calving” from 2 June to 28 June (B), “Summer” from 29 June to 6 September (C), “Fall” from 7 September to 30 November (D), and “Winter” from 1 December to 19 April (E). “Annual” includes year-round movements (F). Map created in ESRI ArcMap version 10.8. Caribou range data from [GNWT et al. \(2016\)](#). Forest line/treeline data from the Arctic Institute of North America ([Timoney et al. 1992](#)). Range planning data from [GNWT \(2018\)](#). Burned area data from [Natural Resources Canada \(2017\)](#).

Fig. 3. Statistically significant trends ($p \leq 0.05$) in maximum annual enhanced vegetation index (Max EVI) across the Bathurst caribou range, 2000–2017. Negative values indicate a significant linear trend over time toward lower values; positive values indicate a significant trend toward higher values. Areas in white did not exhibit significant trends. Burned areas are outlined by grey polygons. Map created in ESRI ArcMap version 10.8. Forest line/treeline data from the Arctic Institute of North America (Timoney et al. 1992). Range planning data from GNWT (2018). Burned area data from Natural Resources Canada (2017).

The length of the growing season increased in 18% of the core annual range of the herd, or 17 268 km² (Fig. 4). This number dropped to 16% (or 15 813 km²) when burned areas were excluded. Increases in season length were due almost entirely to earlier growing season start dates (i.e., earlier green-up) rather than later growing season end dates (i.e., later senescence) (Appendix A, Figs. A1–A4). Increases in growing season length were most prevalent in the spring, calving, and summer portions of the range, which are all predominantly above treeline. Reductions in growing season length (i.e., negative trends) were negligible, occurring in <1% of the core annual range. This was the case regardless of whether burned areas were included or excluded in calculations (Figs. 6 and 7).

Time-integrated EVI, which reflects trends in both growing season length and maximum annual EVI, increased in nearly half (49%) of the core annual range (48 363 km²) (Fig. 5). This number dropped to 44% (43 715 km²) when burned areas were excluded. Increases in time-integrated EVI were particularly prevalent in the spring, calving, and summer (i.e., tundra) portions of the range, occurring in more than 50% of each when burned areas were excluded. Declines in time-integrated EVI within the core annual range were minor (1% of core annual range and 3% of range planning area when burned areas were included and <1% of each when burned areas were excluded) (Figs. 6 and 7).

In general, excluding areas that had burned in the past 60 years reduced the amount of significant productivity and phenology trends (both positive and negative) in the core annual range of the Bathurst herd, although never by more than 5% (Figs. 6 and 7).

Fig. 4. Statistically significant trends ($p \leq 0.05$) in growing season length (LOS) across the Bathurst caribou range, 2000–2017. Negative values indicate a significant linear trend over time toward shorter growing seasons; positive values indicate a significant linear trend toward longer growing seasons. Areas in white did not exhibit significant trends. Burned areas are outlined by grey polygons. Map created in ESRI ArcMap version 10.8. Forest line/treeline data from the Arctic Institute of North America (Timoney et al. 1992). Range planning data from GNWT (2018). Burned area data from Natural Resources Canada (2017).

This is because large portions of the core annual range (i.e., all of the calving, spring, and summer ranges and most of the fall range) are located above forest line, and are therefore unaffected by fire. However, the exclusion of burned areas in the more densely wooded winter range reduced the percentages of significant positive or negative change by between 5% and 15%, depending on the metric (Figs. 6 and 7).

Discussion

Maximum annual EVI, annual growing season length, and annual time-integrated EVI increased significantly on 16%, 18%, and 49% of the herd's core annual range, respectively. Declines were minimal (3%, <1%, and <1%, respectively), meaning that there was an overall directional increase in annual total production over the study period. Trends toward longer growing seasons were driven almost entirely by earlier spring green-up rather than later onset of senescence. All of these trends were similar between the core annual range and the larger range planning area. However, we observed substantial variability in the pattern and magnitude of change across the range. Increases in growing season and time-integrated EVI were most prevalent in tundra regions, which correspond primarily with the calving and summer ranges of the herd. Trends in wooded regions, which correspond primarily with the herd's winter range, were overwhelmingly related to the influence of forest fires, which have burned more than half of the area below forest line since mapping began in 1965.

Fig. 5. Statistically significant trends ($p \leq 0.05$) in time-integrated enhanced vegetation index (TIE) across the Bathurst caribou range, 2000–2017. Negative values indicate a significant linear trend toward lower total annual ecosystem production; positive values indicate a significant linear trend toward higher total annual ecosystem production. Areas in white did not exhibit significant trends. Burned areas are outlined by grey polygons. Map created in ESRI ArcMap version 10.8. Forest line/treeline data from the Arctic Institute of North America (Timoney et al. 1992). Range planning data from GNWT (2018). Burned area data from Natural Resources Canada (2017).

Productivity and phenology trends

The pattern of significant greening we observed in the tundra and forest–tundra ecotone is generally consistent with what other studies have found on the Bathurst Range using different data over longer time frames (e.g., Pouliot et al. 2009; Ju and Masek 2016; Bonney et al. 2018). Using Landsat, Bonney et al. (2018) found that 33% of the tundra portion of their study area underwent significant greening at rates of approximately 0.003 NDVI per year between 1984 and 2016, and Ju and Masek (2016) detected greening of a similar magnitude over the same time period. There is some evidence that rates of tundra greening worldwide were greater in magnitude prior to the early 2000s than they have been since (Bhatt et al. 2013, 2017; Raynolds and Walker 2016). Combined with the shorter time frame of our study, this may explain why the extent of greening we observed was slightly less than it was in these other studies.

A widespread increase in vegetation indices derived from satellite imagery has been observed across the circumpolar north since the early 1980s, and is considered to be among the world's most prevalent global-scale ecological responses to climate change (Myers-Smith et al. 2020). However, as studies using higher resolution data begin to accumulate, it is becoming evident that there is a significant amount of spatial variability in this response (e.g., Ju and Masek 2016; Wang and Friedl 2019). This variability is particularly evident on the Bathurst range. The differences in the herd's seasonal ranges as well as

Fig. 6. Percent of annual and seasonal core use areas of the Bathurst caribou range that exhibited statistically significant trends in the length of growing season (A and B), maximum (Max.) enhanced vegetation index (EVI) (C and D), and time-integrated (T.I.) EVI (E and F) from 2000 to 2017. Breakdown is presented for all areas (left column) and for areas with burned areas excluded (right column). All values exclude areas classified as water. Note that there is some spatial overlap among the different seasonal components of the range (see Fig. 2).

differences between forest, forest–tundra, and tundra zones are demonstrative of regional-scale variability in greening patterns. However, the patchwork of greening we observed within each of these regions demonstrates significant landscape-scale variation as well.

In contrast to several other subarctic studies (Goetz et al. 2005; Beck and Goetz 2012), we did not find evidence of widespread boreal browning (i.e., a decrease in maximum EVI in the boreal forest in the absence of fire). We found that fire greatly increased the prevalence of both significant positive and significant negative trends in maximum EVI, depending on when burns occurred. Areas that burned prior to the start of the satellite record expressed positive trends, while those that burned during the period of record generally expressed negative trends, which is consistent with other studies (Ju and Masek 2016; Bonney et al. 2018; Sulla-Menashe et al. 2018; Wang and Friedl 2019). Given the high prevalence of historic burns in the winter range of the Bathurst herd (i.e., wooded areas), it is difficult to say how

Fig. 7. Percent of regions within the Bathurst caribou range plan that exhibited statistically significant trends in the length of growing season (A and B), maximum (Max.) enhanced vegetation index (EVI) (C and D), and time-integrated (T.I.) EVI (E and F) from 2000 to 2017. Breakdown is presented for all areas (left column) and for areas with burned areas excluded (right column). All values exclude areas classified as water. The three ecological zones (treeline, forest–tundra, and forest) within the range planning area correspond to [Timoney et al. \(1992\)](#).

maximum EVI would have changed in the absence of fire. However, it is worth noting that boreal browning is most prevalent in the drier boreal forests of western Canada and Alaska ([Sulla-Menashe et al. 2018](#); [Potter and Alexander 2020](#)), and that at least some of the boreal browning detected using AVHRR data sets ([Goetz et al. 2005](#); [Beck and Goetz 2012](#)) is not present when trends are derived using Landsat data (e.g., [Ju and Masek 2016](#)). Therefore, it is perhaps unsurprising that we did not observe evidence of boreal browning in unburned portions of the winter range.

Significant advances in the start of the growing season, and corresponding increases in growing season length, were twice as prevalent on tundra portions of the range than they were on unburned portions of the forest–tundra or forest regions. Moreover, the magnitude of seasonal change was also much greater, exceeding a rate of 1 day/year in a large area of the calving and summer ranges between 65°N and 66°N. However, like trends in productivity, significant trends in growing season length were also spatially variable within all of the

seasonal ranges. Variation in phenological trends has been observed in several other studies of growing season length. In a global-scale analysis of growing season duration using AVHRR GIMMS_{3g} data, [Park et al. \(2016\)](#) found large differences in trends between North America and Eurasia, as well as between tundra and boreal biomes. Because of a longer period of analysis, they were also able to detect temporal variation in the data, with earlier onset of season dominating the season length signal prior to 2000, but later senescence being more influential after 2000. This did not occur on the Bathurst range, as we observed very few pixels with significant changes in end of season date. However, it is important to note that different methods of extracting phenological metrics can influence results ([White et al. 2009](#)), as can the choice of satellite data set ([Park et al. 2016](#)), making direct comparisons between trends in phenology among studies particularly difficult.

Interestingly, we found that the length of the growing season often increased in different portions of the core annual range than maximum EVI did. In general, the relationship between phenology and productivity trends is unclear. There is some evidence from both tundra and boreal systems that increases in peak productivity correspond with longer growing seasons and earlier green-up dates ([Bergeron et al. 2007](#); [Arndt et al. 2019](#)). However, other studies have found spatial mismatches between greening and earlier start of season dates similar to what we found in the Bathurst range ([Raynolds et al. 2013](#); [Potter and Alexander 2020](#)). One potential explanation for this is that earlier and more rapid green-up in the spring depletes soil moisture reserves earlier in the growing season, which decreases maximum productivity later in the summer ([Gonsamo et al. 2019](#)). In any case, the spatial mismatch between the two trends in the range of the Bathurst herd explains why the prevalence of significant time-integrated EVI trends (which integrates the two) was so much greater than it was for either one individually. Other studies that have examined additive or time-integrated vegetation indices have found similarly high prevalence of significant positive trends in the tundra ([Park et al. 2016](#); [Potter and Alexander 2020](#)).

The extent to which the trends we observed are driven directly by climate warming as opposed to other environmental factors is unclear. Greening and phenological change have been linked to climate warming in other northern regions ([Bhatt et al. 2010](#); [Forbes et al. 2010](#); [Tan et al. 2013](#); [Berner et al. 2020](#)), and this seems likely for the range of the Bathurst herd given observed increases in mean annual and seasonal temperatures as well as changes in seasonality ([Zhang et al. 2019](#)). However, other variables including vegetation type, terrain features, snow and ice persistence, soil type, and permafrost disturbance strongly mediate the effects of climate change on vegetation and are responsible for the heterogeneity in vegetation trends at landscape scales despite the greater homogeneity of climate change at the same scale ([Bonney et al. 2018](#)). We are currently investigating the importance of these mediating factors using landscape-scale geospatial multivariate analysis (sensu [Chen et al. 2021](#)).

Vegetation change and caribou population dynamics

Our study was not intended to test specific hypotheses for the Bathurst herd's recent decline. Still, the decline of the herd did provide the rationale for the study and the magnitude and pattern of changes we observed are considerable. We therefore reflect briefly here on the potential pathways through which the vegetation change we measured could have contributed to the herd's decline. Several of these hypothesized linkages could form the basis for future studies.

While many factors contribute to their population fluctuations, the synchrony of recent declines in many barren-ground caribou herds suggests the influence of a common and widespread cause. The direct and indirect effects of climate change — including habitat

change — have been implicated in these declines (Mallory and Boyce 2018). Fauchald et al. (2017) examined 35 years of population data for 11 North American herds and compared it with climate indices and summer NDVI derived from AVHRR GIMMS_{3g} data (8 km resolution) over the same period. They concluded that a warmer climate related to reduced sea ice has increased tundra plant biomass, paradoxically leading to a decline in caribou populations because of an expansion of less palatable erect deciduous shrubs. Andruko et al. (2020) found that cover and growth of dwarf birch increased in several different habitat types on the summer range of the Bathurst herd. It is a dominant species of erect shrub across much of the area beyond treeline but it is not a preferred food of caribou as it contains more phenols and less available protein than willows (*Salix* sp.), the other important group of erect shrubs in the region (Thompson and Barboza 2014). Moreover, increases in the abundance of dwarf birch have been linked to significant declines in preferred forage species, including graminoids and lichen (Chagnon and Boudreau 2019). While the greening we observed on the Bathurst range was not ubiquitous, and varied in magnitude, its prevalence in certain core seasonal use areas such as the calving range could have a disproportionate influence relative to other seasonal ranges.

Declines in available forage may also be associated with the changes we observed on the winter range. Lichens comprise between 50% and 75% of barren-ground caribou diet in winter (Lewis et al. 2019). Yet, recovery of lichen after fire can lag significantly behind other vegetation. In a study of the Klaza caribou herd's range in Yukon, Russell and Johnson (2019) estimated that forage lichens took 40–60 years to recover to levels characteristic of caribou winter range. Therefore, wooded areas below treeline that experienced post-fire greening have likely done so without a corresponding increase in winter food availability. And this is most certainly the case for the recently burned areas that exhibited browning trends. Given the cumulative area burned since 1965, it is reasonable to hypothesize that the Bathurst herd was at least partly affected by a reduction in winter food resources.

The changes in phenology we observed may also have affected the Bathurst herd by decoupling the availability of highly nutritious stages of forage plants from periods of high nutritional demand associated with parturition and lactation (Mallory and Boyce 2018). We observed a substantive trend toward earlier green-up on more than 20% of the core calving and core summer ranges, more than 1.5 days per year in some areas. If timing of migration did not also change, then there is potential for this phenological mismatch to lead to negative effects on animal body condition with associated influences on reproduction and survival (Mallory et al. 2020). Using AVHRR phenology data, Chen et al. (2018) found that peak calving dates for the Bathurst herd were linked to range conditions in the previous year as well as the onset of growing season in the current year. They concluded that mismatches between peak forage availability and nutritional demand could have impacted key demographic parameters of the herd.

Although attention has been placed on the potential for habitat change in the form of greening to influence caribou declines, it is also possible that the greening we observed is a consequence of the Bathurst herd's decline. Investigations using remote sensing and plot-level monitoring show that caribou can substantially reduce plant biomass via browsing, grazing, and trampling (e.g., Manseau et al. 1996; Newton et al. 2014). On the range of the Bathurst herd, Zamin and Grogan (2013) demonstrated that experimental exclusion of caribou resulted in a near doubling of biomass of certain preferred forage species. And, using 1 km resolution AVHRR and MODIS data, Rickbeil et al. (2015) found a negative association between caribou density and vegetation productivity between 1986 and 2013.

In 1996, four years prior to the start of our analysis period, the Bathurst herd was estimated at 349 000 animals (GNWT 2019). The plant biomass required to sustain a herd this size is immense. For example, Thompson and Barboza (2014) estimated that a 100 kg

female caribou would require 2.4–8.7 kg of fresh browse daily during the summer. Assuming a similar requirement for males (larger, but less per kilogram energy requirements during summer), then the daily fresh browse required to sustain the herd in 1996 (~349 000 animals) would have been 837.6 and 3036.3 tonnes and would have declined by 97.6% to just 19.7–71.3 tonnes in 2018 (~8200 animals). There are other herbivores in the Arctic that influence ecosystem productivity (e.g., [Johnson et al. 2011](#)), but it seems unlikely that such a large reduction in caribou herbivory over just two decades would have occurred without subsequent changes to primary production. As such, the increases in maximum and time-integrated EVI we observed could be occurring partly in response to, and not entirely because of, the widespread decline in caribou. This is the hypothesis advanced by [Andruko et al. \(2020\)](#), who posit that the expansion of deciduous shrub cover observed in plots on the summer and fall range of the Bathurst herd from 2006 to 2016 was too great to be explained by the climate warming measured during the same period.

Conclusion

The changes we observed in forested portions of the Bathurst caribou range since 2000 are overwhelmingly influenced by forest fires, with the specific response being contingent on time since burn. In contrast, the increases in productivity and advances in phenology we observed on the tundra and forest–tundra portions of the range mirror the wider global phenomenon of Arctic greening ([Myers-Smith et al. 2020](#)). These changes occurred alongside the rapid decline of the herd and, although only correlative at this stage, several possible linkages exist between the two phenomena ([Fauchald et al. 2017](#)). However, the loss of herbivory from the landscape undoubtedly also affected vegetation productivity, and it is challenging to infer causal mechanisms of either landscape change or population change from these trends alone ([Andruko et al. 2020](#)). Determining the nature and magnitude of the relationship between these two phenomena will require spatial–temporal examination of caribou movement and habitat occupation in relation to the observed changes in productivity and phenology (e.g., [Mallory et al. 2020](#)). But these remote, “desktop analyses” do have limitations and need to be complemented by field observations to understand mechanisms of change. Targeted site and plot-level investigations aimed at determining precisely what the remotely observed changes correspond to in terms of plant species composition, establishment, and growth in multiple seasonal ranges are necessary. These field data will also be important for interpreting the potential linkages between remotely derived trends and caribou population dynamics.

Remote sensing of vegetation productivity in Arctic and subarctic regions is a well-established practice. However, sensors have evolved substantially over the last four decades with increased spatial resolution and higher frequency of image acquisition being two of the major advances. This study is one of a growing number of regional-scale analyses that use the MODIS data record. Our results align with the general trends derived from prior studies for the Bathurst caribou range that used data captured at lower spatial resolutions (e.g., AVHRR, [Pouliot et al. 2009](#)) or longer intervals (e.g., Landsat, [Bonney et al. 2018](#)). However, by using MODIS data, we were able to measure both productivity and phenology metrics at a spatial resolution more meaningful for resource management. Our findings show substantial spatial heterogeneity in long-term vegetation trends not previously evident and demonstrate that increases in peak productivity do not necessarily coincide with increases in growing season length in northern regions. Studies that rely on satellite data with low temporal resolution or that focus solely on maximum annual productivity can miss these important aspects of regional vegetation change.

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Appendix A appears on the following pages.

Appendix A

Fig. A1. Statistically significant trends ($p \leq 0.05$) in the start of growing season (SOS) date across the Bathurst caribou range, 2000–2017. Negative values indicate a linear trend toward an earlier date; positive values indicate a linear trend toward a later date. Areas in white did not exhibit statistically significant trends. Burned areas are outlined by grey polygons. Map created in ESRI ArcMap version 10.8. Forest line/treeline data from the Arctic Institute of North America (Timoney et al. 1992). Range planning data from GNWT (2018). Burned area data from Natural Resources Canada (2017).

Fig. A2. Statistically significant trends ($p \leq 0.05$) in the end of growing season (EOS) date across the Bathurst caribou range, 2000–2017. Negative values indicate a linear trend toward an earlier date; positive values indicate a linear trend toward a later date. Areas in white did not exhibit statistically significant trends. Burned areas are outlined by gray polygons. Map created in ESRI ArcMap version 10.8. Forest line/treeline data from the Arctic Institute of North America (Timoney et al. 1992). Range planning data from GNWT (2018). Burned area data from Natural Resources Canada (2017).

Fig. A3. Percent of annual and seasonal core use areas of the Bathurst caribou range that exhibited statistically significant trends in the start of the growing season (A and B) and end of the growing season (C and D) from 2000 to 2017. Breakdown is presented for all areas (left column) and for areas with burned areas excluded (right column). All values exclude areas classified as water. Note that there is some spatial overlap among the different seasonal components of the range (see Fig. 2).

Fig. A4. Percent of regions within the Bathurst caribou range plan that exhibited statistically significant trends in the start date of the growing season (A and B) and the end date of the growing season (C and D) from 2000 to 2017. Breakdown is presented for all areas (left column) and for areas with burned areas excluded (right column). All values exclude areas classified as water. The three ecological zones (treeline, forest–tundra, and forest) within the range planning area correspond to [Timoney et al. \(1992\)](#).