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Changing northern vegetation conditions are influencing barren ground caribou (*Rangifer tarandus groenlandicus*) post-calving movement rates

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Abstract

Aim: To quantify changes in vegetation productivity over the past three decades across five barren ground caribou (*Rangifer tarandus groenlandicus*) herd ranges and assess how these changes are influencing caribou movement rates.

Location: Northwest Territories and Nunavut, Canada.

Methods: As an indicator of vegetation productivity, the enhanced vegetation index (EVI) was calculated on newly developed cloud-free, gap-free, Landsat surface reflectance image composites representing 1984–2012. Changes in EVI were assessed on a pixel basis using Theil-Sen's nonparametric regression and compared across herd ranges and land cover types using generalized least squares regression. Animal movement velocity was calculated from caribou telemetry data and generalized additive mixed models were used to link movement rates with vegetation productivity during the post-calving phase of the year (July and August).

Results: Vegetation productivity increased across the five caribou herd ranges examined. The largest productivity increase occurred over the ranges of the most western herds, with the largest observed changes in grassland or shrub habitats. Caribou tended to move more slowly through tundra habitats with elevated levels of productivity to a point, while grasslands movement rates decreased linearly with increasing productivity. Movement velocities peaked at intermediate productivity levels in shrub habitats.

Main conclusions: Over the three decades of collected data, barren ground caribou habitats have become more productive, which is consistent with other studies that have documented increases in Arctic vegetation productivity. The more western herds, whose ranges are also closest to the Arctic Ocean, experienced the largest increases in productivity. Finally, we demonstrate that barren ground caribou movement patterns will likely change as a result of changing vegetation productivity in complex manners depending on herd, habitat type and the magnitude of change in vegetation productivity.

KEYWORDS
animal movement, Arctic, EVI, forest/tundra productivity, herbivory, Landsat, telemetry

1 | INTRODUCTION

Ecological changes being documented in Arctic, sub-Arctic and boreal terrestrial environments are among the most rapid on Earth (Chapin et al., 2000; Kelly et al., 2013; Price et al., 2013; Serreze et al., 2000). Fire regimes in the western boreal forest have shifted considerably even in the past 50 years (de Groot, Flannigan, & Cantin, 2013; Joly, Stuart Chapin, & Klein, 2010; Kelly et al., 2013) with some locations showing a doubling of annual area burned over the past four decades (Kasischke & Turetsky, 2006). Tall shrub proliferation has rapidly transformed many areas of the low Arctic (Lantz, Gergel, & Henry, 2010; Myers-Smith et al., 2011). In the Tuktoyaktuk Coastlands, the growth and proliferation of green alder (*Alnus viridis*) and dwarf birch (*Betula nana exilis*) has significantly reduced the extent of lichen and graminoid-dominated tundra within several decades (Fraser, Lantz, Olthof, Kokelj, & Sims, 2014). Myers-Smith et al. (2011) documented increased shrub expansion at the northern limits of many shrub communities, indicating that warming climates may be driving shrub proliferation. However, there was extensive spatial variation for the climate–shrub expansion association leading the authors to conclude that soil moisture may limit shrub expansion in certain locations. Based on measurements from multiple data sources including remotely sensed data, large portions of Arctic tundra are becoming productive, likely as a result of longer growing seasons that have resulted in increased productive vegetation (Chapin et al., 2000; Euskirchen et al., 2006; Kimball, McDonald, & Zhao, 2006; Myers-Smith et al., 2011; Xu et al., 2013).

Changes in vegetation of this magnitude are likely to profoundly impact northern wildlife. Barren ground caribou (*Rangifer tarandus groenlandicus*) are the most numerous large mammal in the Canadian north (Bergerud, 2000) and are circumpolar in their global distribution (Vors & Boyce, 2009). They are long-distance migrants (Berger, 2004; Festa-Bianchet, Ray, Boutin, Cote, & Gunn, 2011; Vors & Boyce, 2009), calving on shores of the Arctic Ocean and commonly overwintering several hundred kilometres to the south in the northern boreal forest (Bergerud, 2000; Gustine et al., 2014; Joly, Duffy, & Rupp, 2012). Barren ground caribou are grouped into herds based on their fidelity to calving grounds (Gunn & Miller, 1986; Schaefer, Bergman, & Luttich, 2000) with certain herds numbering in the hundreds of thousands (Bergerud, 2000). Each of the five herds considered here (described in more detail in Methods) has experienced a significant reduction in herd size since over the past three decades (Adamczewski et al., 2014; Nagy & Johnson, 2006), in some cases by more than an order of magnitude (i.e. the Bathurst herd, Boulanger, Croft, & Adamczewski, 2014).

Barren ground caribou's annual migration allows them to access young, highly nutritious vegetation during spring (Bergerud, 2000; Heard, Williams, & Melton, 1996), to avoid predators during calving (Heard et al., 1996), and to lessen parasite loads/avoid parasitism (Folstad, Nilssen, Halvorsen, & Andersen, 1991; Hughes, Albon, Irvine, & Woodin, 2009). As large mammalian herbivores, barren ground caribou respond directly to vegetation conditions across their range (Bergerud, 2000), making documentation of range conditions paramount to conservation efforts. Overgrazing on summer ranges has been proposed as a cause of herd decline for wild barren ground caribou (George River herd; Manseau, Huot, & Crete, 1996). Semi-domesticated reindeer in Fennoscandinavia have been shown to influence tundra and forest vegetation conditions (Kitti, Forbes, & Oksanen, 2009; Olofsson, Kitti, Rautiainen, Stark, & Oksanen, 2001; Tveraa, Stien, Bardsen, & Fauchald, 2013); however, the concept of overgrazing is an elusive and debated concept for these managed herds (Mysterud, 2006).

Since vegetation dynamics directly affect barren ground caribou, changes in the composition, biomass or forage quality of vegetation communities are expected to lead to changes in caribou behaviour. For instance, increasing biomass due to shrub proliferation may result in landscapes that are more difficult for caribou to travel through. Terricolous lichens forms the major portion of caribou diets during winter in the boreal forest (Joly et al., 2010); and recent studies suggest that increased shrub cover is reducing lichen cover and biomass (Fraser et al., 2014). Tussock cottongrass (*Eriophorum vaginatum*) forms a major portion of the spring diet in caribou (Cebrian, Kielland, & Finstad, 2008; Jandt, Joly, Randy Meyers, & Racine, 2008), and shrub expansion in some regions is reducing the cover of this species (Fraser et al., 2014). Additionally, the two species of tall deciduous shrubs (dwarf birch (*Betula nana*) and green alder (*Alnus viridis*)) which were found to be expanding in terms of range in the Tuktoyaktuk Coastlands (Fraser et al., 2014) are not preferred forage species of caribou being well defended chemically from herbivory (Christie et al., 2015). However, caribou will selectively forage on certain shrub species (e.g. species of willow (*Salix* spp.); Heard et al., 1996; Christie et al., 2015); encroachment of shrub species which offer some nutritional benefit may not result in the same magnitude of lost forage opportunities.

Due to factors including remoteness, growing season length and cost, gathering in situ data on vegetation dynamics across the range of barren ground caribou herds presents substantial difficulties. Herd ranges encompass thousands of square kilometres of habitat in remote areas that are expensive to assess (Berger, 2004; Bergerud, 2000). Additionally, if habitat changes are to be documented, repeat measures of habitat conditions over time are required. These challenges are encouraging the development of novel methods for tracking habitat conditions in the north that involve using ex situ data such as space-borne remote sensing (Falldorf, Strand, Panzacchi, & Tømmervik, 2014; Rickbeil, Coops, & Adamczewski, 2015; Rickbeil, Hermosilla, Coops, White, & Wulder, 2016). There are multiple remote sensing platforms and sensors that can be employed for habitat change analysis. The Moderate Resolution Imaging Spectroradiometer (MODIS) onboard NASA satellites Terra and Aqua is an attractive option that offers a wide range of environmental spectral indices and has a rapid revisit time allowing for both within-year and between-year changes to be quantitatively documented. However, MODIS data is spatially coarse (250–1,000 m pixel sizes), and due to its 1999 launch, it has data products available from 2000 onwards. The data can be combined with longer term NOAA-AVHRR imagery to extend the archive; however, there are issues with sensor compatibility, including the match between spectral channels, spatial resolution and radiometric bit depth, among other issues (Fontana et al., 2012).

A less-explored option, particularly in northern environments, is data from the Landsat series of satellites. Landsat offers a finer spatial resolution (30 m), with greater spatial detail at a cost of a narrower swath width and longer revisit times between acquisition opportunities (Wulder et al., 2008). This can result in challenges due to the combined effects of actual acquisitions (e.g. number of images collected for a given location) and collection date (phenology represented) combined with atmospheric effects (i.e. cloud, shadow, haze contamination). Since the advent of the Landsat programme in 1972, Canada has been an active International Cooperator, receiving and archiving images for the Canadian landmass, with well over 600,000 images available representing all Landsat sensors (White & Wulder, 2014). Internationally, Canada is among the nations with the most spatially and temporally dense representation of Landsat imagery (Wulder et al., 2016). The 2008 opening of the Landsat archive (Woodcock et al., 2008) has fostered the development of highly sophisticated and consistent image-processing routines that maximize the information content of the archive (Hansen & Loveland, 2012; Wulder & Coops, 2014). As an example, new pixel-based compositing approaches have emerged to produce spatially contiguous, cloud-free, radiometrically consistent surface reflectance image composites, combining multiple Landsat scenes (Griffiths, Linden, Van Der Kuemmerle, & Hostert, 2013; Hermosilla, Wulder, White, Coops, & Hobart, 2015; White et al., 2014). Gap-free image composites and annual change data are now available across Canada, removing one of the major barriers to assessing caribou habitat in the north using Landsat data.

The objective of this study is to document changes in barren ground caribou habitat, specifically vegetation productivity, and assess how changes in vegetation productivity affect caribou movement rates using a productivity index generated from comprehensive, annual, Landsat-derived 30-m data. Since the measure of productivity used here was collected in summer (July and August), it is most directly applicable to the post-calving portion of the year, which occurs at the same time (Nagy, 2011). Additionally, post-calving is a period where access to forage and forage quality are critical for adding fat and providing milk to calves making a post-calving assessment of vegetation productivity's association with movement rates not only appropriate given the data but also ecologically important. Based on previous research, we anticipate that vegetation productivity will have increased across all herd ranges (Fauchald, Park, Tømmervik, Myneni, & Hausner, 2017; Kimball et al., 2006; Myers-Smith et al., 2011). However, our hypothesis is that rates of increase in vegetation productivity will be larger in locations that have or are currently transitioning from tundra to shrub-dominated habitat (for habitat definitions see Methods—Land cover data). Shrub proliferation is occurring in many locations across the low Arctic (Fraser et al., 2014; Lantz et al., 2010; Myers-Smith et al., 2015), and these transition zones offer the largest potential increase in vegetative cover and greenness and are sensitive to warming climates (Epstein et al., 2004). We hypothesize that increasing vegetation productivity in tundra and grassland habitats will result in reduced movement rates owing to increased forage biomass availability while increasing productivity in shrub habitats will lead to elevated movement rates due to reduced forage opportunities and increased insect harassment.

2 | MATERIALS AND METHODS

2.1 | Study area

The five herds examined here are located in the Northwest Territories and Nunavut, Canada. Their winter range extends into the northern Boreal forest, while their summer ranges and calving grounds occur on the continental tundra north of the treeline. Collectively, the area these five herds utilize is approximately 700,000 km^2. From west to east, these herds are known as the Cape Bathurst, Bluenose West, Bluenose East, Bathurst and Ahiak/Beverly (see Figure 1 for generalized herd ranges developed using 95% minimum convex polygons applied to herd telemetry data).

2.2 | Caribou data

Depending on the herd, GPS collar data collection was initiated between 2006 and 2008 following through to 2012 (the end of the Landsat time series discussed below). Fix intervals (the length of time between successive relocations) were either 5 hr or 8 hr. The 5-hr data were associated entirely with the Bathurst herd, and as such only 5-hr data were used to calculate movement rates for the Bathurst herd. All other movement rates for all other herds were derived from 8-hr data. Variation in movement rates by herd (either due to actual movement rate differences between herds or differences owing to differing fix intervals (Pépin, Adrados, Mann, & Janeau, 2004) was addressed by including herd as a random effect in the generalized additive mixed models (GAMMs; Zuur, Ieno, Walker, Savliev, & Smith, 2009) (see the Statistical Analyses—Caribou movement section in Methods for details). Fix rates (the percentage of successful GPS fixes) varied from a low of 93.0% in tundra habitats to 95.0% in forested habitats; all points following a missed fix were discarded. Individual animals were included in the subsequent analysis provided they had accumulated at least one full year of data. In total, 258 animals had been tracked for 1 year or more at time intervals of 8 or fewer hours. A maximum of 66 individuals were available for the Bluenose West herd and a minimum of 30 individuals for the Ahiak/Beverly herd.

2.3 | Landsat pixel-based compositing

Recently, White et al. (2014) developed a pixel-based image compositing method that selects best available pixels (BAP) using a series of pixel scoring functions. These functions score each pixel observation for (1) Landsat sensor, (2) acquisition day of year, (3) distance to

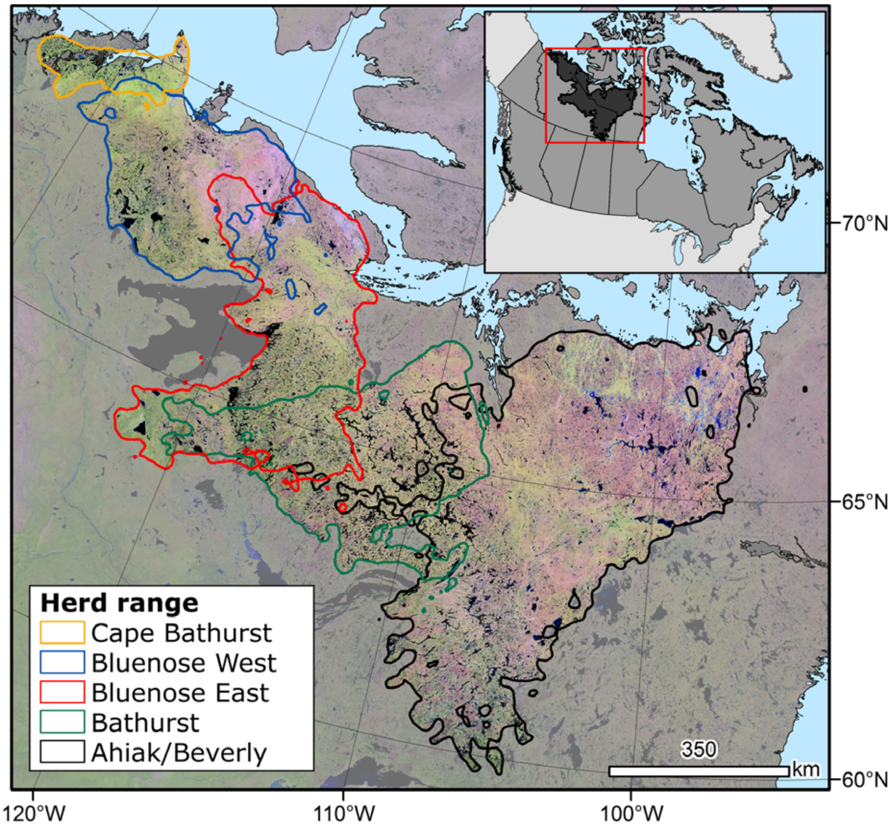

FIGURE 1 The five barren ground caribou (*Rangifer tarandus groenlandicus*) herds examined here with outlined generalized herd ranges occurring in the Northwest Territories and Nunavut, Canada. The background image is a Landsat 2011 false-colour composite (Bands: 5, 4, 3) centred on August 1st at 30 m spatial resolution [Color figure can be viewed at wileyonlinelibrary.com]

clouds and cloud shadows and (4) atmospheric opacity. Pixel observations with the highest scores are then included in the BAP image composites for a given year. Pixels where there are no data available that meet the BAP criteria are labelled as data gaps. Using pixel-level temporal screening, further anomalies (e.g. haze or undetected clouds) are identified and flagged as noise. Using the time series data for each pixel (1984–2012), proxy infill values are generated for data gaps and noisy pixels following the methods presented in Hermosilla et al. (2015), to create gap-free surface reflectance image composites (Figure 2a). The results are Canada-wide annual Landsat image composites with no data gaps from 1984 to 2012 centred on August 1st of a given year Hermosilla et al. (2016).

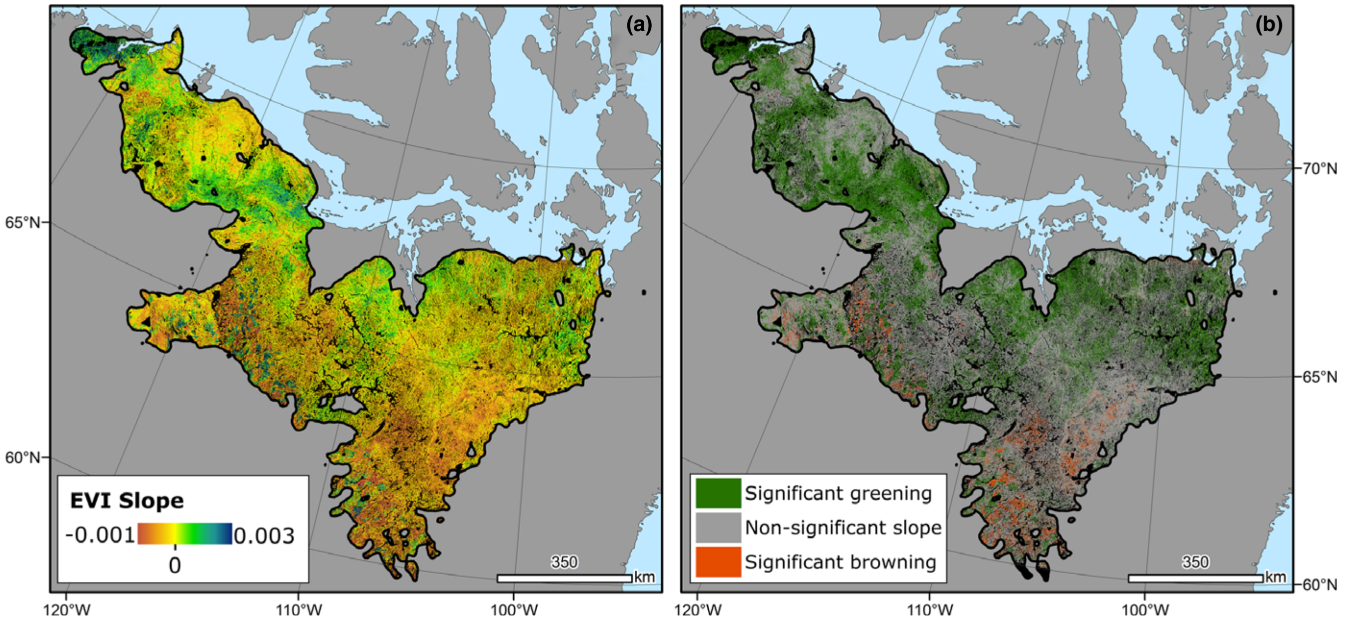

FIGURE 2 (a) EVI Theil-Sen's slopes and (b) Mann-Kendall significance tests for across all five herd ranges. Greening indicates a significant positive slope while browning indicates a significant negative slope [Color figure can be viewed at wileyonlinelibrary.com]

The enhanced vegetation index (EVI) was calculated yearly from the visible and near-infrared bands in the composite images to represent vegetation productivity conditions across caribou ranges. EVI (Huete et al., 2002) has been shown across a range of studies to be highly correlated to primary production throughout the growing season at hardwood and conifer-dominated sites globally (Sims et al., 2008). Similar to the normalized difference vegetation index (NDVI), EVI employs the red and near-infrared bands to estimate primary productivity. However, EVI also employs the blue band and three coefficients to correct for atmospheric and vegetation canopy influences on pixel reflectance values. Xiao, Zhang, Hollinger, Aber, and Moore (2005) further demonstrated that EVI is more sensitive than NDVI in identifying subtle changes in the seasonal dynamics of leaf phenology.

2.4 | Land cover data

Land cover data were derived from the Canada Center for Remote Sensing's annual MODIS land cover product, which describes 19 land cover classes across Canada at 250-m spatial resolution from 2001 to 2011 (Pouliot, Latifovic, Zabcic, Guindon, & Olthof, 2014). The 2011 year was used to represent current conditions, while all forest classes (temperate or sub-polar needleleaf; sub-polar taiga needleleaf forest; temperate or sub-polar broadleaf deciduous; mixed forest) shrub classes (temperate and sub-polar; polar shrubland), grassland (temperate and sub-polar; polar grassland) and tundra classes (sub-polar or polar barren-lichen-moss) were simplified to produce a forest, shrub, grass and tundra land cover map at 250 m spatial resolution (see Table 1 for land cover class distributions between herd ranges), which was then resampled to a 30 spatial resolution to match that of Landsat. For the post-calving movement analyses only, tundra, grassland and shrub habitats were assessed owing to the lack of telemetry data occurring in forested areas during this time.

2.5 | Statistical analyses

2.5.1 | EVI across herd ranges

Changes in annual EVI were assessed using Theil-Sens (TS) nonparametric regression (Fraser et al., 2014; Michaud, Coops, Andrew, & Wulder, 2012; Sen, 1968) (Figure 2b). The TS approach calculates all pairwise slopes for a given variable through time by pixel throughout the image stack (1984–2012) and then returns the median slope as a change metric. TS slopes are less sensitive to outliers than traditional linear regression and, as a result, are becoming more commonly used in time series analyses at the pixel level (Michaud et al., 2012; Rickbeil et al., 2015). Slope significance was determined using nonparametric Mann–Kendall tests (Fraser et al., 2014; Kendall, 1975).

TABLE 1 Percentage of each vegetated land cover class by herd range for the year 2011

Land cover	Ahiak (%)	Bathurst (%)	Bluenose East (%)	Bluenose West (%)	Cape Bathurst (%)
Lichen/moss	16	2	7	12	3
Grassland	70	52	63	51	62
Shrub	5	9	8	4	27
Forest	9	37	23	33	3

To examine variation in EVI TS slopes for each herd, 200 random samples were then taken from each land cover class from each herd's range. Pixels containing water were eliminated and land cover and EVI slope values were extracted. These values were then analysed in a generalized least squares regression (GLS) with a maximum-likelihood iterator, built using the package "nlme" (Pinheiro, Bates, DebRoy, & Sarkar, 2013) in R 3.4.2 (R Core Team, 2013). A GLS model was used as it allows for the inclusion of spatial autocorrelation functions to account issues with spatially structured model residuals (Zuur et al., 2009). Variable selection began with full models incorporating all variables (land cover type and herd) with an interaction term. The Interaction term was then removed and both models were compared using a likelihood ratio test to select the most parsimonious model (Zuur et al., 2009). Both models were assessed for spatially structured residuals using semi-variograms. Since both models displayed spatially structured residuals, Gaussian spatial correlation structures were added and the models were subsequently re-examined.

2.5.2 | Caribou movement

Individual barren ground caribou movement velocities were associated with EVI values during the post-calving phase of the year—July and August (Nagy, 2011)—for tundra, grassland and shrub habitats. GAMMs with a negative binomial link to account for over-dispersion in the data. GAMMs allow for nonlinear responses to be appropriately estimated while assigning unique animal identifiers nested within herd as random effects, thereby accounting for repeated measures per animal (Ciuti et al., 2012) and variation in movement velocities between herds. 1,000 samples were taken from each herd for each habitat class, when possible. In some cases, less than 1,000 points were available for a particular herd in a particular habitat class; if there were over 500 data points available, all points were retained for the particular habitat model. Less than 500 points resulted in a herd being excluded from that habitat's model. When a herd was included in a particular model with less than 500 data points, a lack of model convergence tended to occur. When sample sizes were reduced to maintain equal sampling across all herds, singular models tended to occur owing to the complex nature of the nested random effects and small sample sizes. As a result, the tundra movement analysis lacked data from the Bathurst herd (272 data points) and the grasslands analysis lacked data from the Ahiak/Beverly herd (92 data points). Model residuals were tested for spatial autocorrelation using semi-variograms (Zuur et al., 2009). All models had significant levels of spatial autocorrelation in their residuals, and

Gaussian spatial correlation structures were, therefore, added to the GAMM models (Zuur et al., 2009).

3 | RESULTS

3.1 | EVI across herd ranges

In all cases, the number of significant positive EVI TS slopes was greater than the number of significant negative EVI TS slopes (Table 2). The Cape Bathurst herd had the highest percentage significant positive slopes (53.4%), while the Bluenose West herd had the lowest percent negative slopes (0.7%). The Ahiak/Beverly herd had both the lowest percent positive slopes (24.5%) and the highest percent negative slopes (5.7%).

EVI TS slopes were found to vary significantly across herd ranges and land cover types (*F* = 6.57, *p* < .001), with a significant interaction detected between the herd range and land cover type (Log Likelihood Ratio = 69.14, *p* < .001) compared with the model lacking an interaction term (Figure 3). The final model also included a Gaussian spatial autocorrelation structure. The Cape Bathurst and Bluenose West herds had the largest overall TS slopes, with the shrub class in the Cape Bathurst herd having the largest median EVI slope. The median TS slope (0.0015) for the Cape Bathurst shrub class would result in a 13% increase in mean shrub EVI values (mean shrub EVI = 0.33) across a 28-year period. Across all herd ranges either grass or shrub land cover classes had the largest median EVI slopes. Generally, EVI slopes became increasingly negative following a west to east gradient across herd ranges and in no case did a median EVI slope fall below zero.

TABLE 2 The percentage of significant positive, negative and non-significant Theil-Sen's slopes across each herd's range

Herd	% Positive	% Negative	% Non-significant
Cape Bathurst	53.4	1.0	45.6
Bluenose West	45.0	0.7	54.3
Bluenose East	38.2	3.7	58.1
Bathurst	29.5	4.1	66.4
Ahiak/Beverly	24.5	5.7	69.8

3.2 | Caribou movement

Caribou tended to move most slowly, on average, through shrub habitats (median velocity = 171 m/hr, 0.05 quantile = 23 m/hr, 0.95 quantile = 1,123 m/hr) when compared with tundra (median velocity = 491 m/hr, 0.05 quantile = 69 m/hr, 0.95 quantile = 1,637 m/hr) and grassland habitats (median velocity = 349 m/hr, 0.05 quantile = 40 m/hr, 0.95 quantile = 1,609 m/hr). In tundra habitats, caribou movement rates decreased (*F* = 3.60, *p* = .04, RMSE = 493 m/hr) with increasing EVI values until an EVI value of approximately 0.3 after which movement rates did not change with increasing EVI values (Figure 4; see Appendix S1 for a plot containing raw data points). Caribou movement rates declined in nearly linear fashion in grassland habitats with increasing EVI values (*F* = 9.96, *p* = .002, RMSE = 524 m/hr). Movement rates in shrub habitats peaked at intermediate EVI values, approximately EVI = 0.33 (*F* = 2.39, *p* = .05, RMSE = 431 m/hr).

4 | DISCUSSION

Consistent with our hypothesis, our results indicate that forest, shrub, grassland and lichen/moss vegetation communities across all five herd ranges became more productive from 1984 to 2012. The percentage of significant positive slopes greatly outweighed the percentage of significant negative slopes for each herd; EVI had significantly increased in more than half the pixels in the Cape Bathurst's range. The increase in productivity detected here is consistent with multiple studies that have examined Arctic vegetation productivity, all of which indicate a greening of the Arctic that is generally

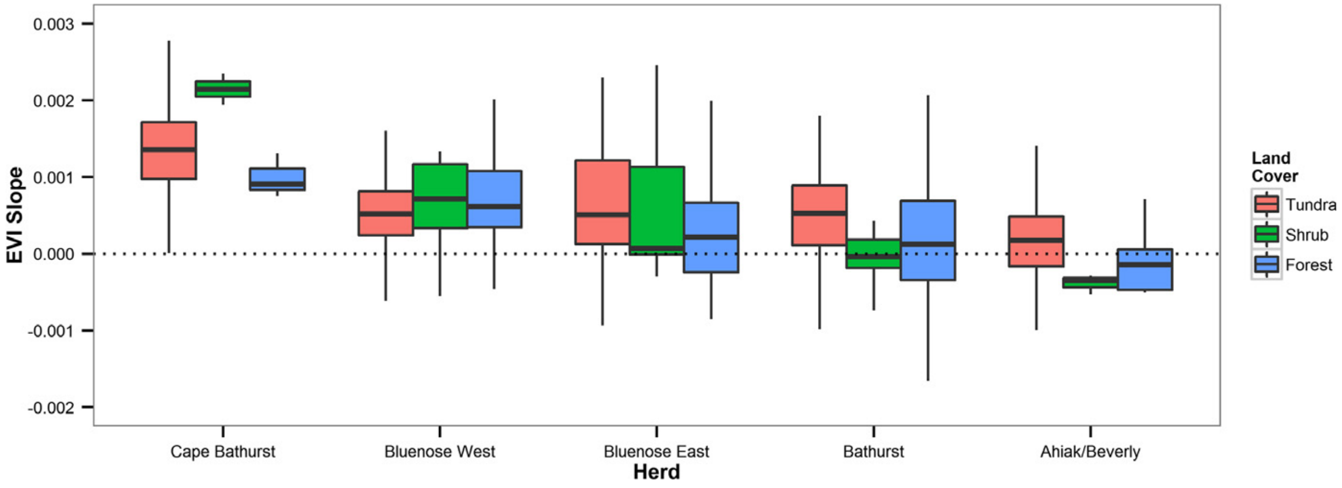

FIGURE 3 Boxplots (.5, .25, .5, .75. 95 delineations) of Theil-Sen's EVI slopes for forest, grass, shrub and lichen/moss land cover classes across the five herds examined here [Color figure can be viewed at wileyonlinelibrary.com]

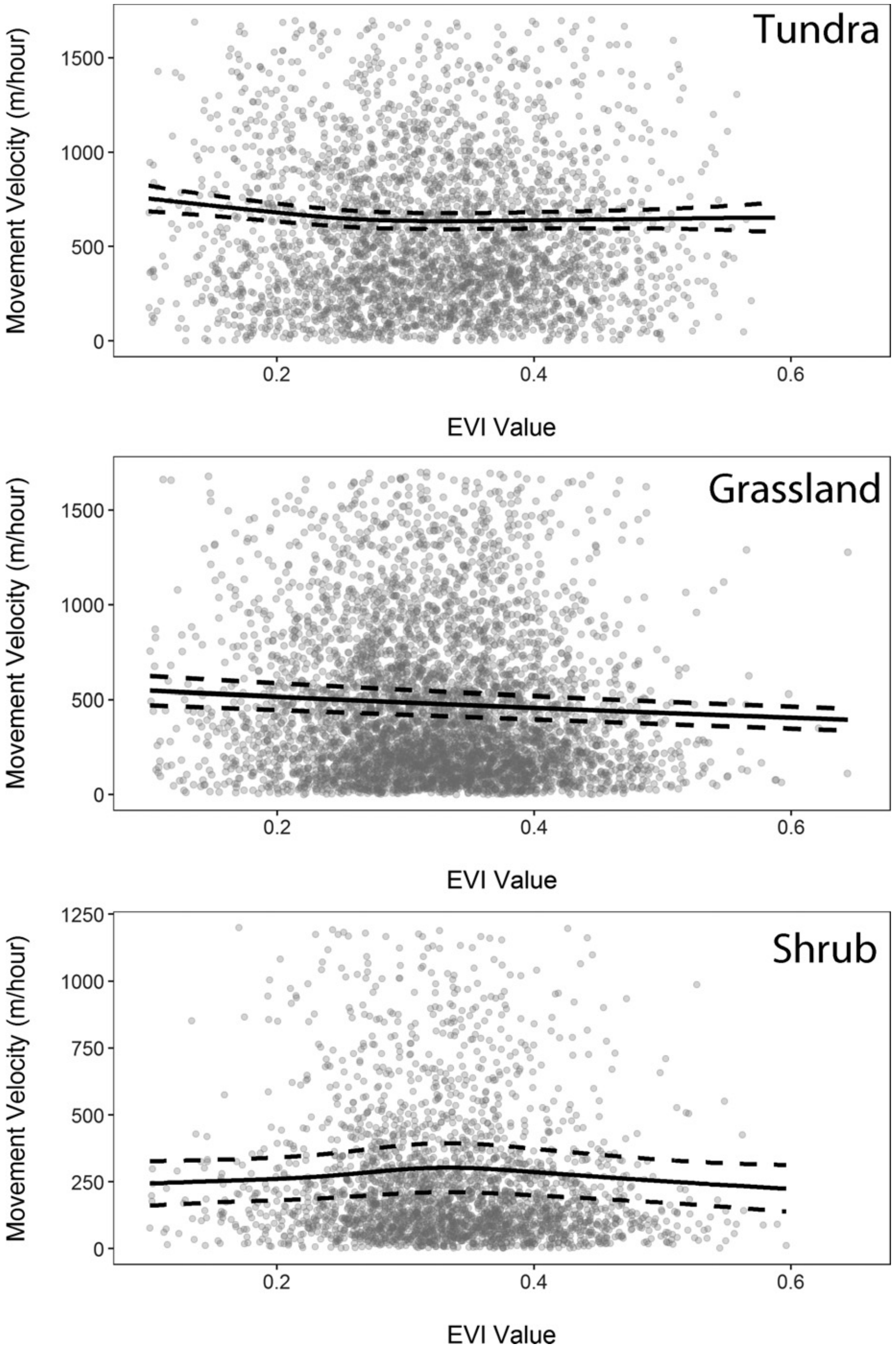

FIGURE 4 Predicted GAMM relationships (solid lines) and data points for caribou movement velocities versus EVI values in tundra, grassland, and shrub land cover classes. Dotted lines represent one standard error from the mean prediction. The *y*-axis is limited to the 95th percentile of estimated movement velocities

associated with increased growing season length, particularly in spring (Bhatt et al., 2010; Guay et al., 2014; Raynolds, Comiso, Walker, & Verbyla, 2008; Stow et al., 2004). Importantly, this productivity signal was detected using only Landsat imagery avoiding any issues of data compliance between sensors which may occur when combining data across sensors such as AVHRR and MODIS (Fontana et al., 2012).

Measured productivity responses were not, however, uniformly consistent across the landscape. Vegetation productivity increased more rapidly and had a greater percentage of positive significant slopes in the western herd ranges. Increases in productivity were most pronounced in shrub habitats in the western herds, while grassland habitats displayed the largest increases in productivity in the more eastern herds. Bhatt et al. (2010), Post et al. (2013), and Fauchald et al. (2017) all linked increases in Arctic vegetation productivity to earlier sea ice melt, and the western herds are closer, on average, to the Arctic Ocean than the eastern herds. Further, Fauchald et al. (2017) found that while vegetation biomass has increased across herd summer ranges in North America, this increase has not been accompanied by an increase in herd abundance suggesting a minimal or net negative effect from increasing biomass on summer ranges. The authors suggest that the increase has been driven primarily by the expansion of shrub species which do not provide forage for caribou and instead reduce forage on herd summer ranges. Macias-Fauria, Forbes, Zetterberg, and Kumpula (2012), however, detected a link between sea ice melt and vegetation productivity in early spring only and attributed increased Arctic vegetation productivity more to increasing early summer air temperatures.

There is a marked divide in the surficial materials present on the eastern edge of Great Bear Lake (Shaw, Sharpe, Harris, Lemkow, & Pehleman, 2010), which also generally divides the Bluenose West and Cape Bathurst herds from the three more eastern herds. The majority of the surficial materials west of Great Bear Lake in the Taiga Plains Ecozone are made up of thick continuous surface till, while east of Great Bear Lake the Taiga Shield Ecozone is predominantly ancient bedrock rock and thin, divided till. The higher rates of vegetation productivity increase could be linked to deeper and more widespread tills found in the more western herd ranges. Macias-Fauria et al. (2012) detected depressed levels of vegetation productivity in *Salix lanata* in nutrient-poor, sand-dominated substrates. Similarly, Myers-Smith et al. (2015) detected elevated shrub productivity in soils with greater soil moisture retention capacity. Additionally, the continentality, resulting in colder temperatures, of the eastern herd ranges may also play a role in limiting shrub recruitment (Lantz et al., 2010). The higher rate of increase in shrub and tundra habitats is consistent with the multiple studies documenting shrub proliferation in tundra habitats (Lantz, Marsh, & Kokelj, 2013; Stow et al., 2004), whereby low productivity lichen/moss/grass land cover types are shifting towards birch- and alder-dominated land cover types, becoming more productive in the process (Fraser et al., 2014). Myers-Smith et al. (2015) found that shrub expansion was greatest at the northern margins of shrub communities indicating that climatic warming is indeed affecting some shrub communities. However, the authors also document extensive spatial variation in how arctic shrub communities are responding to changing climatic conditions and suggest that variation in soil moisture can limit shrub communities' response to warming.

When animals forage, they tend to move slowly in a random search pattern; when they are movement focused, caribou tend to move quickly in a more linear fashion. Measuring the velocity of movement (Calenge, Dray, & Royer-Carenzi, 2009; Dodge, Weibel, & Lautenschütz, 2008) allows for inferences to be made regarding whether the animal was primarily engaged in foraging behaviour or movement (Zollner & Lima, 1999). However, there are numerous other factors other than foraging which can affect barren ground caribou movement patterns (see Hebblewhite and Haydon 2010 for a general summary of GPS collar limitations), including but not limited to: predator and insect avoidance (Hagemoen & Reimers, 2002; Weladji, Holand, & Almøy, 2003), rutting, and landscape features such as impassable terrain and water. Therefore, while movement rates may reflect foraging behaviour, we limit our assessment to movement velocities and the potential influences of vegetation productivity.

Barren ground caribou moved more slowly in more productive lichen/moss and grassland habitats. As a foraging species, this seems intuitive, especially considering the amount of tussock cottongrass (Cebrian et al., 2008; Jandt et al., 2008) and lichen (Bergerud, 2000) consumed as forage. While the ability of EVI to act as an appropriate proxy measure for lichens is unknown, EVI will detect elevated productivity in cottongrass species. If movement velocities in these two habitats do reflect some degree of foraging activity, increasingly levels of vegetation productivity in grassland habitats may result in increased foraging opportunities for caribou, while in tundra habitats, our results indicate that any gain due to increased productivity are likely to occur only in low productivity tundra habitats.

Caribou displayed a different reaction to elevated levels of productivity in shrub habitats, travelling most rapidly through intermediately productive shrub habitats. Although caribou do selectively forage on shrub species (Hansen, Henriksen, Aanes, & Sæther, 2007), many shrub species are not primary forage and therefore will not promote vigorous foraging activities. We suspect that shrub density may be an important (and unmeasured) factor here, with open shrub habitat supporting some lichen growth while dense shrub habitats may suppress both lichen growth and force slow movement rates. We hypothesized that insect harassment would play an important role in movement velocities in shrub habitats (Hagemoen & Reimers, 2002; Weladji et al., 2003); however, shrub movement velocities were considerably lower than tundra or grassland movement velocities. It is possible that rather than forcing caribou to move rapidly through shrub environments, insect harassment forces caribou to exposed ridges and eskers or to north aspect slopes which have retained some snow to avoid parasitism which subsequently reduces their movement rates.

5 | CONCLUSIONS

While tracking change in Arctic environments is a challenging process, it is a critical one. Vegetation conditions directly influence the ability of barren ground caribou to forage, move across a landscape and avoid predators. Newly developed remote sensing products offer exciting and novel opportunities for researchers to integrate detailed vegetation data with caribou data on an annual basis at a spatial scale relevant for individual animals.

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DATA ACCESSIBILITY

The seamless Landsat reflectance composite imagery produced by the "National Terrestrial Ecosystem Monitoring System (NTEMS):

Timely and detailed national cross-sector monitoring for Canada" project will soon be available from the Government of Canada and is currently viewable at: forests.foundryspatial.com. Forest change data from the NTEMS project is available at: https://opendata.nfis.org/mapserver/nfis-change_eng.html. All source Landsat imagery is available from the United States Geological Survey. The barren ground caribou telemetry data are available by request through Government of Northwest Territories Wildlife Management Information System (http://www.enr.gov.nt.ca/programs/wildlife-research/wildlife-management-information-services).

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BIOSKETCH

The Integrated Remote Sensing Studio (IRSS) is located in the Faculty of Forestry at the University of British Columbia. IRSS investigates the application of remote sensing and spatial data for questions surrounding biodiversity, biogeography and conservation. Details of our work can be found at http://irsslab.forestry.ubc.ca/.

Author contributions: All authors developed the research question and hypotheses. TH, NCC, MAW, JCW produced the NTEMS data. GJMR conducted the movement analyses. All authors wrote the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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