Biophysical Determinants of Shifting Tundra Vegetation Productivity in the Beaufort Delta Region of Canada

Jordan H. Seider, Trevor C. Lantz, Txomin Hermosilla, Michael A. Wulder, and Jonathan A. Wang

School of Environmental Studies, University of Victoria, Victoria, British Columbia, Canada; Canadian Forest Service (Pacific Forestry Centre), Natural Resources Canada, Victoria, British Columbia, Canada; Department of Earth System Science, University of California, Irvine, California, USA

ABSTRACT

Temperature increases across the circumpolar north have driven rapid increases in vegetation productivity, often described as ‘greening’. These changes have been widespread, but spatial variation in their pattern and magnitude suggests that biophysical factors also influence the response of tundra vegetation to climate warming. In this study, we used field sampling of soils and vegetation and random forests modeling to identify the determinants of trends in Landsat-derived Enhanced Vegetation Index, a surrogate for productivity, in the Beaufort Delta region of Canada between 1984 and 2016. This region has experienced notable change, with over 71% of the Tuktoyaktuk Coastlands and over 66% of the Yukon North Slope exhibiting statistically significant greening. Using both classification and regression random forests analyses, we show that increases in productivity have been more widespread and rapid at low-to-moderate elevations and in areas dominated by till blanket and glaciofluvial deposits, suggesting that nutrient and moisture availability mediate the impact of climate warming on tundra vegetation. Rapid greening in shrub-dominated vegetation types and observed increases in the cover of low and tall shrub cover (4.8% and 6.0%) also indicate that regional changes have been driven by shifts in the abundance of these functional groups. Our findings demonstrate the utility of random forests models for identifying regional drivers of tundra vegetation change. To obtain additional fine-grained insights on drivers of increased tundra productivity, we recommend future research combine spatially comprehensive time series satellite data (as used herein) with samples of high spatial resolution imagery and integrated field investigations.

Key words: Landsat; random forests; remote sensing; low arctic; arctic tundra; greening; EVI; climate change; land cover.
Over 70% of the Beaufort Delta region has exhibited significant greening. Geology, topography, and land cover mediate the response of tundra vegetation to warming. Shifts in productivity are associated with shifts in the cover of shrub-dominated terrain.

**INTRODUCTION**

Increasing temperatures in the Arctic (Arctic Monitoring and Assessment Programme [AMAP] 2004; Serreze and others 2009; Johannessen and others 2016; Davy and others 2018), while regionally variable in magnitude, are driving rapid changes to the structure and composition of tundra vegetation. Plot-based and fine-scale remote sensing studies have documented shifts in the dominant vegetation, with deciduous shrubs now proliferating in what was once lichen- and graminoid-dominated tundra (Elmendorf and others 2012; Ropars and Boudreau 2012; Lantz and others 2013; Moffat and others 2016; Travers-Smith and Lantz 2020). Vegetation productivity can also be measured at broad scales using multispectral satellite vegetation indices (Gao and others 2000) such as the Enhanced Vegetation Index (EVI) and the Normalized Difference Vegetation Index (NDVI). Changes in these indices have been observed across the Arctic with increasing productivity referred to as ‘tundra greening’ (Jia and others 2003; Bhatt and others 2010; Epstein and others 2012). Continental and pan-Arctic scale changes in vegetation productivity have generally been attributed to rapid temperature increases at high latitudes (Jia and others 2003; Bhatt and others 2010; Miller and Smith 2012; Fraser and others 2014a; Berner and others 2020). Plot-scale warming experiments and repeated observation also provide evidence that vegetation change has been caused by increasing temperature (Chapin and others 1995; Walker and others 2006; Hudson and Henry 2009; Elmendorf and others 2012).

At the landscape-scale, research suggests that variability in soil moisture, land cover type, and landscape position are responsible for the heterogeneous response of Arctic vegetation productivity (Ropars and Boudreau 2012; Tape and others 2012; Martin and others 2017; Bonney and others 2018; Campbell and others 2021). In this study, we explore the environmental factors driving heterogeneity in vegetation productivity trends across the Beaufort Delta region by combining plot-based fieldwork with an analysis of the Landsat satellite archive (Wulder and others 2019). We use a random forests (RF) ensemble decision tree algorithm to determine the environmental factors influencing spatial heterogeneity in tundra productivity trends in the Beaufort Delta region. Ultimately, we seek to understand how variation in environmental conditions influences the spatial patterns of vegetation productivity at a landscape-scale. An improved understanding of factors mediating tundra vegetation change will contribute to local and regional planning and inform earth system models that include feedbacks between vegetation growth and ecological processes such as permafrost dynamics, albedo, and evapotranspiration (Verseghy 1991; Verseghy and others 1993; Verseghy 2000; Bonan and others 2003; Quillet and others 2010).

**STUDY AREA**

This study focuses on the tundra ecosystems across the Yukon North Slope (0.54 MHa) and Tuktoyaktuk Coastlands (2.92 MHa). These Low Arctic ecosystems are located in the Beaufort Delta region of the western Canadian Arctic (Figure 1a). This coastal region borders the Beaufort Sea to the north and is bounded by the northern edge of the subarctic forest to the south (Timoney and others 1992). Both regions are located within the Inuvialuit Settlement Region and are significant to the communities of Tuktoyaktuk (population of 900), Inuvik (population of 3200), and Aklavik (population of 600), who use these lands for hunting.
fishing, trapping, traditional harvesting of plants, and other cultural practices (Alunik and Morrison 2003; Murray and others 2005; Tyson and others 2016).

The Yukon North Slope extends from the foothills of the Richardson Mountains to the coast of the Beaufort Sea. Areas at high elevation drain to the Beaufort via the deeply incised canyons of the Babbage, Blow, and Big Fish Rivers among others (Rampton 1982; Yukon Ecoregions Working Group [YEWG] 2004). Rolling hills and hummocky terrain dominate the eastern portion of the Yukon North Slope that ends in a steep escarpment at the Mackenzie Delta (Rampton 1982). Average annual temperature between 1984 and 2016 at Shingle Point was $-9.2 \, ^\circ C$ with an average summer temperature (June through August) of 9.0 $^\circ C$ (Environment and Climate Change Canada [ECCC] 2018b). On average, Shingle Point received 254 mm of precipitation annually (ECCC 2018b), about half of which fell as rain (Burn and Zhang 2009). The Tuktoyaktuk Coastlands extend from the eastern limit of the Mackenzie Delta to Cape Bathurst to the east. This gently rolling landscape is

Figure 1. a Study area and site locations from the 2019 field season with inset showing the extent the map in the context of northwestern Canada and Alaska, USA. b Surficial geology classes comprising greater than 1% of the study area (Fulton 1989) and c elevation in metres (Porter and others 2018) used in random forests analyses across the study area.
scattered with lakes and ponds and is characterized by hummocky terrain in upland areas and polygonal terrain and wetlands at lower elevations (Rampton 1988; Ecosystem Classification Group [ECG] 2012). The climate at Tuktoyaktuk is similar to Shingle Point, with average annual and summer temperatures between 1984 and 2016 of −9.4 °C and 8.9 °C, respectively (ECCC 2018a). Average total precipitation during this period was 146 mm, about 40% of which fell as rain (ECCC 2018a). The Yukon North Slope and Tuktoyaktuk Coastlands are separated by the low-lying alluvial terrain in the Mackenzie Delta ecoregion. This dynamic ecosystem was excluded from our study area because much of it is forested and the tundra communities present are strongly influenced by hydrological dynamics (Gill 1972, 1973; Pearce 1986; Burn and Kokelj 2009).

The Yukon North Slope hosts a diversity of terrain types including coastal beaches and estuaries, low-lying wetlands, upland tussock tundra, and shrub tundra (YEWG 2004; Wang and others 2019). The upland tundra in the foothills of the Richardson Mountains occurs on well-drained soils that support characteristic communities of tall and dwarf shrubs, lichens, graminoids and forbs (YEWG 2004). The Tuktoyaktuk Coastlands are largely covered by shrub and tussock tundra with wetter areas dominated by sedge and moss tundra (ECG 2012; Moffat and others 2016). In the southern portion of this region, scattered spruce woodlands are located along sheltered creeks and other low-lying areas (Lantz and others 2019).

Both the Yukon North Slope and Tuktoyaktuk Coastlands are underlain by continuous permafrost and are characterized by thermokarst features including polygonal terrain, earth hummocks, thaw slumps and pingos (Rampton 1982, 1988; YEWG 2004; ECG 2012). The Laurentide Ice Sheet covered most of this region during the Wisconsinan glaciation with the exception of land south and west of the Richardson Mountains in northern Yukon and the northern tip of the Tuktoyaktuk Peninsula and Cape Bathurst (Jessop 1971; Hughes and others 1981; Duk-Rodkin and Hughes 1995; YEWG 2004; ECG 2012).

**METHODS**

To investigate the drivers of vegetation change in the Beaufort Delta region, we combined RF modelling of regional EVI trends with multivariate analyses of plot-scale field data. We classified pixel-based trends in EVI (1984–2016) as: (1) exhibiting significant increases in EVI or (2) un-trended. We used these binary classes (increasing EVI/un-trended EVI) as response variables in a classification RF model to determine the factors facilitating and constraining increased productivity. To identify the factors influencing the magnitude of greening, we also performed a regression RF model that predicted the slope of significant positive EVI trends. To facilitate site selection for field sampling and multivariate analyses, pixels exhibiting significant increases in EVI were further classified as moderate or high magnitude greening.

**EVI Trend Analysis**

To document changes in the productivity of tundra vegetation across the study area, we tracked changes in EVI using the Landsat satellite archive (1984 – 2016). EVI is a modified form of NDVI in which the blue band of the visible spectrum and satellite-specific correction terms (C₁, C₂, and L) account for soil (L) and atmospheric/aerosol (C₁ and C₂) influences (Gao and others 2000).

$$EVI = 2.5 \times \frac{NIR - RED}{NIR + (C_1 \times RED) - (C_2 \times BLUE) + L}$$

(1)

We used EVI in this analysis because it is sensitive to differences in vascular plant phytomass and vascular plant net primary productivity (Kushida and others 2015) and it performs well across a range of soil moisture conditions (Raynolds and Walker 2016). We obtained the EVI trend surface from Chen and others (2021) who generated the trend surface using annual composite Landsat images from 1984 to 2016. These images were obtained using the Composite2Change method for selecting best-available-pixels from the Landsat archive to produce a gap-free surface reflectance raster for each year (Hermosilla and others 2016). The imagery used to produce best-available-pixel composites was cross-calibrated among Landsat sensors (see: Markham and Helder 2012; Hermosilla and others 2016). Composite imagery was used to calculate EVI on a pixel basis (30-m spatial resolution) for each year and a pixel-based, non-parametric Theil-Sen regression was performed on the resulting time series (Theil 1950; Sen 1968) using the EcoGenetics package (Roser and others 2017) in R (R Core Team 2019). The significance of pixel-based slopes was assessed using a Mann–Kendall test for monotonic trends (Mann 1945; Kendall 1948) performed using the Kendall package in R (McLeod 2011). In our analysis, we used the resulting p-values to determine whether significant change ($p < 0.05$) had occurred in each pixel from 1984 to 2016.
We also used the raster surface derived from Theil-Sen regression of EVI trends to classify the study area into site types exhibiting: (1) high greening, (2) moderate greening, (3) no significant change (stable sites), and (4) browning (see histogram: Supplementary Fig. 1) for the purpose of our field investigation. Areas showing non-significant EVI trends ($p > 0.05$) were classified as stable. Pixels with significant increases in EVI were further classified based on the slope of the EVI trend. Pixels with slopes that were within one standard deviation (SD; $1.45 \times 10^{-3}$ per year) of the mean EVI trend ($< 2.24 \times 10^{-3} + SD$ per year) were classified as moderate greening, and pixels with an increase greater than one standard deviation above the mean EVI trend ($> 2.24 \times 10^{-3} + SD$ per year) were classified as high greening. Pixels with a significant negative slope (decline in EVI over time) were classified as browning. Since browning pixels only accounted for 0.63% of pixels in the study area, we did not consider this class as a category in this analysis.

Random Forests Analysis and Variable Importance

To identify the biophysical variables that best explain spatial variation in EVI trends, we used two RF models (Breiman 2001). RF models are decision-tree based, ensemble machine-learning methods involving the assembly of many regression or classification trees using a subset of available data to increase predictive capability (Breiman 2001; De’ath 2007). The RF method can also be used to determine variable importance by measuring the mean decrease in model accuracy upon removal of a given variable (Cutler and others 2007). In our first analysis, we used a classification RF to discriminate pixels showing a significant increase in EVI ($p < 0.05$, positive slope) from untrended pixels ($p > 0.05$). In a second analysis, we used a regression RF to model the magnitude of the change in EVI (Theil-Sen regression slope) of pixels exhibiting significant increases in EVI ($p < 0.05$, positive slope) using the same suite of biophysical variables. We created both models using the randomForest package (Liaw and Wiener 2002) in R. Explanatory variables used in each model are presented in Table 1. We ran the classification RF model using a random selection of 40,000 pixels of each class to ensure balanced sampling. For the regression RF, we used a random sample of 1% (66,442 pixels) of all pixels in the study area. We ran each model using 1000 trees and calculated the variable importance using the importance function (Liaw and Wiener 2002). We assessed the influence of the four variables that had the largest impact on model accuracy using partial dependence plots showing the marginal effect of a given variable on the modelled parameter while keeping all other variables constant (Friedman 2001; Hastie and others 2009). For the classification RF, our partial dependence plots show the probability of significant greening. The partial dependence plots for a regression RF show the predicted magnitude of the slope in the EVI trend.

Explanatory Variables

Broad-scale biophysical data used in this study were obtained from a variety of sources and data processing and aggregation were completed using the R statistical software (Table 1: R Core Team 2019). We selected explanatory variables known to affect growth and productivity but were not able to directly assess the influence of microclimate because suitable data are not available to adequately capture climate variability at such fine scales. A digital elevation model (DEM), with 2-m spatial resolution (Figure 1c), was sourced from the Polar

| Table 1. Explanatory Variables Used in Random Forests Modelling |
|---|---|---|---|
| **Explanatory variables** | **Units** | **Resolution** | **Source** |
| Elevation | metres | 2 m | PGC ArcticDEM (Porter and others 2018) |
| Slope | degrees | 2 m | PGC ArcticDEM derivative |
| Topographic Wetness | index | 2 m | PGC ArcticDEM derivative |
| Topographic Position | index | 2 m | PGC ArcticDEM derivative |
| Terrain Ruggedness | index | 2 m | PGC ArcticDEM derivative |
| Solar Insolation | index | 2 m | PGC ArcticDEM derivative |
| Land Cover (1984) | category | 30 m | NASA ABoVE (Wang and others 2019) |
| Surficial Geology | category | 20 m² | Fulton 1989 |

*20 m resolution corresponds to the smallest size polygon (approximately 20 m²) in the original source data.*
of the study area (class descriptions can be found in Supplementary Tables 1 and 2). Spatial resolution of the data sources described above was matched to the EVI trend data (30 m). Where resolution of a dataset was finer than 30 m, cells were aggregated by taking the mean of sub-pixels. We resampled continuous data using a bilinear interpolation method while categorical data used the nearest neighbour method. These operations were performed with the resample function from the raster package (Hijmans 2020). Surficial geology and elevation data are shown in Figure 1b and c, and all other explanatory variables can be found in Supplementary Fig. 2.

Field Surveys

To assess the influence of biophysical variables on recent changes in tundra productivity, we measured biotic and abiotic variables at sites across the study area. Field sites were selected by randomly choosing 40 points in each of the productivity classes defined using the EVI trend (moderate greening, high greening, and stability). Randomization was constrained such that the pixel (30 m²) containing the selected point was surrounded by the same greening class. We visited 21 stable sites, 32 moderate greening sites, and 26 high greening sites in July and August of 2019 (Figure 1a). At each site, we measured a suite of biotic and abiotic variables, as described below.

Vegetation surveys and soil sampling were conducted along two 30-m transects. Transects were orientated in north–south and east–west directions such that the 15-m mark on both transects was centered on the predetermined site coordinate. These dimensions were selected to create a plot corresponding to the 30-m resolution of one Landsat pixel. Thaw depth and soil moisture were measured at 5-m intervals along each transect as well as inside all vegetation quadrats at a site. We measured soil moisture at 3–5 cm below the surface using a handheld moisture probe (Delta-T Devices HH2 Moisture Meter with ML3 ThetaProbe Soil Moisture Sensor). Thaw depth was measured using a graduated metal probe inserted into the ground until the depth of refusal. We visually estimated the percent cover of plant species or species groups inside nested 5 m² and 1 m² quadrats at four locations at every site. We positioned quadrats using a random point located inside each of the four quadrants of the cross transect (northwest, northeast, southwest, and southeast). We estimated the cover of upright shrubs and trees
using the larger quadrat and the cover of dwarf shrubs, graminoids, herbaceous species, lichens, and bryophytes using the smaller quadrat.

When vegetation cover estimates were completed, we collected a composite active layer soil sample from within each quadrat using a small shovel. The profile exposed during sample collection was also used to estimate the thickness of the moss layer and organic soil horizon. Soil samples were stored at \(-20\, ^\circ\text{C}\) before they were submitted for analysis of gravimetric soil moisture, macronutrients including nitrogen and phosphorus, and micronutrients including magnesium, sulphur and calcium. Chemical analyses were carried out using an inductively coupled plasma mass spectrometer (ICP-MS) at the Chemical Services Laboratory at the Pacific Forestry Centre of the Canadian Forest Service in Victoria, British Columbia.

Vegetation Community and Environmental Data Analysis

To explore differences in community composition among sites exhibiting different levels of landscape scale greening, we used non-metric multidimensional scaling (NMDS) ordination. We applied a log\((x + 1)\) transformation to the raw vegetation percent cover data and ran the NMDS using a Bray–Curtis dissimilarity matrix of the transformed percent cover data. This analysis was set to repeat 100 times and select the best two-dimensional representation of the original data. The NMDS was performed using the \textit{metaMDS} function from the \textit{vegan} package (Oksanen and others 2019) in R. We used the analysis of similarities (ANOSIM; Clarke 1993) function (\textit{anosim}) from \textit{vegan} (Oksanen and others 2019) to test for statistically significant differences in vegetation community composition among the three sites types (stable, moderate greening, and high greening). To identify the species making the greatest contribution to differences among site types, a similarity percentage (SIMPER) analysis was conducted using the \textit{simper} function in the \textit{vegan} package (Oksanen and others 2019). We also compared the cover of vegetation classes in 1984 and 2014 using the multiyear land cover classification presented in Wang and others (2019). Specifically, we calculated the percent cover of land cover classes in 1984 and 2014 and compared the differences across the entire study area and between the Yukon North Slope and Tuktoyaktuk Coastlands.

**RESULTS**

**Study Area Response Overview**

Approximately 70% of the study area showed significant increases in EVI between 1984 and 2016 (Figure 2, Table 2). Split across the study area, 71% of the Tuktoyaktuk Coastlands showed significant greening compared to 66% of the Yukon North Slope (Table 2). The Tuktoyaktuk Coastlands also had a higher average EVI trend than the Yukon North Slope but was similar to the average across the entire study area (Table 2).

**Classification Random Forests Analysis**

The top four predictors in the classification RF were surficial geology, elevation, land cover in 1984, and TWI (Figure 3). This model had user's accuracy of 72.05% and was capable of classifying pixels as stable and greening with user's accuracy of 73.5% and 70.6%, respectively. The area under the curve (AUC) of the receiver operating characteristic (ROC) is 0.796 (see Supplementary Fig. 3).

Partial dependence plots for surficial geology show that till blanket, glaciofluvial complex, glaciofluvial plain, and lacustrine sand were more likely to exhibit greening than colluvial and alluvial materials, which had a greater probability of being stable (Figure 4a). The partial dependence plot for elevation shows that the greatest probability of greening occurred at elevations between 0 to 60 m (Figure 4b). Elevations above approximately 60 m had a higher probability of being stable. This analysis also showed that significant greening was most likely in low shrub, tussock tundra, and sparsely vegetated land cover classes, while tall shrub, fen, and barren cover classes were more likely to be stable (Figure 4c). With respect to topographic variables, the partial dependence plot for topographic wetness (TWI) indicates an increased probability of greening at moderate landscape wetness (Figure 4d). Values of TWI greater than 7.5 are largely associated with the margins of ponds and lakes as well as coastal tundra areas on the Tuktoyaktuk Peninsula.

**Regression Random Forests Analysis**

The four most important variables in the regression RF, which predicted the magnitude of greening, were surficial geology, elevation, and land cover, and TWI followed by a suite of variables related to topography (Figure 5). This model explained
20.41% of the variance in EVI trend based on the out-of-bag data. The partial dependence plots for the regression RF show that lacustrine sands, till blanket, and glaciofluvial complex cover are associated with more rapid greening (Figure 6a). Areas underlain by fine colluvium and till veneer had rates of EVI change lower than the average value (3.07 $\times 10^{-3}$ per year) for significantly trended pixels (Figure 6a). Areas covered by till blanket comprised roughly 46% of the entire study area, of which, over 51% are significantly greening (Table 3).

### Table 2. Greening Responses Across the Study Area

| Region                | Area (km$^2$) | Percent of region greening (%) | Mean EVI trend in region (per year) |
|-----------------------|---------------|--------------------------------|-------------------------------------|
| Entire Study Area     | 34,627        | 70.2                           | $2.239 \times 10^{-3}$              |
| Tuktoyaktuk Coastlands| 29,184        | 71.1                           | $2.274 \times 10^{-3}$              |
| Yukon North Slope     | 5443          | 66.2                           | $2.097 \times 10^{-3}$              |

Figure 2. Raw EVI trends (from Chen and others 2021) where un-trended and browning pixels are grey and brown, respectively. The inset at the top left shows the extent of the main map in the context of northwestern Canada and Alaska, USA.

Figure 3. Variable importance in the classification random forest (predicting probability of significant greening) measured as the mean decrease in model accuracy scaled by the standard error of the change in model accuracy.
Vegetated land cover classes exhibited the greatest predicted EVI trends (Figure 6c). The mean EVI trends across low shrub and tussock tundra classes were greater than the average EVI trend of significantly greening pixels (Table 4). The predicted EVI trend as a function of TWI decreased with higher index values, dropping below the average mean EVI trend of significantly greening pixels at approximately TWI of 8 (Figure 6d).

**Vegetation Community Analysis**

The NMDS ordination shows that heterogeneity in plant community composition was higher in the Tuktoyaktuk Coastlands compared to the Yukon North Slope. Moderate and high greening sites sampled in the Yukon had community composition that was largely indistinguishable from stable sites ($R_{ANOSIM} = 0.039$, $P_{ANOSIM} < 0.05$), whereas the Tuktoyaktuk Coastlands exhibited greater differentiation between sites with moderate and high greening ($R_{ANOSIM} = 0.27$, $P_{ANOSIM} = 0.001$; Figure 7).

In the Tuktoyaktuk Coastlands, stable and high greening sites exhibited significant differences in community composition ($R_{ANOSIM} = 0.27$). This difference was driven largely by greater abundance of *Ledum decumbens*, *Betula spp.*, and *Vaccinium vitis-idaea* at high greening sites (Table 5). Conversely, we observed greater cover of lichens, *V. uliginosum*, *Arctostaphylos spp.*, and *Salix spp.* at stable sites (Table 5).

---

### Table 3. Summary of Enhanced Vegetation Index (EVI) Trends (per year) by Surficial Geology Class in Order of Proportional Cover of Study Area (Fulton 1989)

| Class              | Mean EVI trend of significantly greening pixels | Standard deviation of EVI trend in significantly greening pixels | Proportion of study area (%) | Proportion of class that is significantly greening (%) |
|--------------------|-----------------------------------------------|---------------------------------------------------------------|-----------------------------|-------------------------------------------------------|
| Till Blanket       | $3.24 \times 10^{-3}$                        | $1.13 \times 10^{-3}$                                       | 46.54                       | 51.58                                                 |
| Glaciofluvial Plain| $2.80 \times 10^{-3}$                        | $1.13 \times 10^{-3}$                                       | 16.66                       | 16.71                                                 |
| Fine Colluvial     | $2.58 \times 10^{-3}$                        | $1.29 \times 10^{-3}$                                       | 11.75                       | 7.74                                                  |
| Till Veneer        | $2.55 \times 10^{-3}$                        | $9.79 \times 10^{-4}$                                       | 8.49                        | 7.39                                                  |
| Lacustrine Sand    | $3.46 \times 10^{-3}$                        | $1.15 \times 10^{-3}$                                       | 5.84                        | 6.15                                                  |
| Glaciofluvial Complex| $3.18 \times 10^{-3}$                    | $1.05 \times 10^{-3}$                                       | 5.54                        | 6.31                                                  |
| Alluvial           | $3.00 \times 10^{-3}$                        | $1.62 \times 10^{-3}$                                       | 3.66                        | 3.21                                                  |
| **All Classes**    | **$3.07 \times 10^{-3}$**                    | **$1.19 \times 10^{-3}$**                                   | -                           | -                                                     |

The last column shows the proportion within each class that exhibited significant greening.

### Table 4. Summary of Enhanced Vegetation Index (EVI) Trends (per year) by Land Cover Class in Order of Proportional Cover of Study Area (Wang and others 2019)

| Class              | Mean EVI trend of significantly greening pixels | Standard deviation of EVI trend in significantly greening pixels | Proportion of study area (%) | Proportion of class that is significantly greening (%) |
|--------------------|-----------------------------------------------|---------------------------------------------------------------|-----------------------------|-------------------------------------------------------|
| Herbaceous         | $3.00 \times 10^{-3}$                        | $1.14 \times 10^{-3}$                                       | 29.08                       | 27.66                                                 |
| Low Shrub          | $3.24 \times 10^{-3}$                        | $1.06 \times 10^{-3}$                                       | 26.33                       | 28.92                                                 |
| Sparserly Vegetated| $2.94 \times 10^{-3}$                        | $1.24 \times 10^{-3}$                                       | 13.89                       | 14.34                                                 |
| Tall Shrub         | $2.95 \times 10^{-3}$                        | $1.26 \times 10^{-3}$                                       | 13.13                       | 11.80                                                 |
| Tussock Tundra     | $3.21 \times 10^{-3}$                        | $1.02 \times 10^{-3}$                                       | 11.68                       | 13.30                                                 |
| Barren             | $2.27 \times 10^{-3}$                        | $2.44 \times 10^{-3}$                                       | 2.20                        | 1.13                                                  |
| Woodland           | $2.91 \times 10^{-3}$                        | $1.53 \times 10^{-3}$                                       | 1.49                        | 1.27                                                  |
| Fen                | $2.75 \times 10^{-3}$                        | $1.29 \times 10^{-3}$                                       | 1.48                        | 1.37                                                  |
| **All Classes**    | **$3.07 \times 10^{-3}$**                    | **$1.19 \times 10^{-3}$**                                   | -                           | -                                                     |

The last column shows the proportion within each class that exhibited significant greening.
Analysis of data from Wang and others (2019) indicates that sparse and herbaceous cover decreased by 7.5% and 6.2% across the entire study area between 1985 and 2014. These data also show that low shrub and tall shrub cover increased by 4.8 and 6.0% over this period (Figure 8). The pattern of vegetation change was similar in both regions, but the magnitude of increases in shrub-dominant terrain were higher in the Tuktoyaktuk than the Yukon North Slope. The decline in herbaceous cover was also greater in the Tuktoyaktuk Coastlands compared to the Yukon North Slope (Figure 8).

**DISCUSSION**

Landscape-scale variation in surficial materials, topography, and vegetation structure were good predictors of changing tundra productivity because these factors influence access to both moisture and soil nutrients. Surficial materials govern the development of tundra soils and control nutrient and moisture availability. Parent materials impact soil formation through differential weathering and the mineral and chemical composition of the substrate (Brady and Weil 1996; Walker 2000). Poorly sorted materials such as till veneer are often associated with exposed bedrock and are found at higher elevations in the foothills of the Richardson Mountains and on the Anderson Plain (Fulton 1989). These thin tills contain larger gravel and boulders and result in shallow, poorly developed soils that are unable to retain moisture and nutrients (Brady and Weil 1996). Till veneer was associated with stable vegetation in our study area, while the deeper soils that typically develop in areas of till blanket or glaciofluvial complexes were associated with greening (Figure 4a) and had higher EVI trend values than the average across the study area (Table 3). Finer-grained soils at lower elevation have a larger surface area, are less susceptible to leaching, and are able retain more nutrients for plant uptake (Walker and Everett 1991; Brady and Weil 1996).

The importance of elevation in our RF models indicates that microclimatic variation associated with landscape position also impacts tundra vege-
Our observation that lower rates of greening and a reduced probability of greening were associated with higher elevations suggests that cold temperatures, dry soils, and reduced snowpack on hilltops limit the effects of increasing regional temperatures on tundra productivity. Soils at higher elevation also tend to have more unconsolidated sediments and exposed bedrock, which likely limit productivity because of reduced moisture and nutrients.

Differences in relative elevation drive variation in soil moisture that likely influence vegetation community development and productivity. Previous research shows that landscape scale variation in temperature, soil moisture and snow accumulation can impact the establishment and growth of tundra plants (Sturm and others 2001; Myers-Smith and others 2011; Niittynen and others 2020a; Niittynen and others 2020b). Our NMDS analysis also showed an association between elevated soil moisture and plant community composition at moderate and high greening sites (Figure 7). A number of recent studies have demonstrated that soil moisture influences tundra vegetation growth (Myers-Smith and others 2015; Cameron and Lantz 2016; Ackerman and others 2017; Bjorkman and others 2018) and indices of vegetation productivity (Campbell and others 2021; Chen and others 2021). Topographic variation in microclimate and soil moisture have also been shown to be better predictors of tundra greening at fine scales than broader-scale climate-related factors such as the total length of growing season (Gamon and others 2013). Soil moisture levels influenced by microclimate can drive increased nutrient mineralization and are likely an important mechanism of increased productivity (Chapin and others 1988; Deslippe and Simard 2011; Deslippe and others 2012; Mekonnen and others 2021). More rapid greening associated with moderate levels of topographic wetness indicate that tundra vegetation on mesic to moist soils is most sensitive to regional warming. This is likely because moderate soil moisture limits the negative effects of temperature-induced moisture stress on tundra growth and productivity (Johnson and Caldwell 1975; Dagg and Lafleur 2011; Myers-Smith and others 2015; Ackerman and others 2017). Snowmelt associated with the onset of spring can also increase soil moisture in areas of large drifts, contributing to an influx of moisture to tundra soils. Gamon and others (2013) found that earlier snowmelt was associated with drier soils and lower mid-season NDVI which highlights the complex interaction between moisture availability and growing season. Winter conditions (notably snow cover) are also important to consider since winter is a crucial period in the development of vegetation communities and their functional diversity (Niittynen and others 2020a; Niittynen and others 2020b).

Vegetation type was a good predictor of EVI trends because some functional groups, such as

![Figure 6. Partial dependence plots for the top four variables used in the regression random forest predicting EVI trend (per year): a Quaternary surficial geology (Fulton 1989), b elevation in metres (Porter and others 2018), c land cover in 1984 (Wang and others 2019) and d topographic wetness index. Note differing y-axis ranges among plots A-D. The dashed line on the y-axis in plots B and D highlights the mean EVI trend value for significantly greening pixels (3.07 × 10⁻³ per year). Plots B and D are presented with decile rug marks of training data.](image-url)
shrubs and graminoids, are more responsive to changes in temperature and soil conditions. Specifically, many species of deciduous shrub are adapted to respond to changes in nutrients availability, the length of the growing season, and moisture availability at the onset of spring (Chapin and others 1995; Hobbie and Chapin 1998; Bret-Harte and others 2001; Myers-Smith and others 2011; Kelsey and others 2020). Increased productivity in shrub tundra communities was likely also driven by the ability of deciduous shrubs to rapidly allocate resources to secondary growth and asexual reproduction (Bret-Harte and others 2001; Wiedmer and Senn-Irlet 2006; Ropars and Boudreau

Figure 7. Non-metric multidimensional scaling (NMDS) ordination of vegetation community composition across the a Yukon North Slope (stress = 0.15) and b Tuktoyaktuk Coastlands (stress = 0.13). Sites split by classification with stable, moderate greening, and high greening shown as blue, green, and red points and polygons, respectively with abiotic vectors ($p < 0.1$) overlaid. The ordinations also plot associations between species and functional type (lichen) to cumulative contribution of 65% and NMDS score. Species abbreviations are defined in Table 5.
Taller, shrub dominated vegetation may also increase soil moisture and nutrient availability via increased snow capture (Sturm and others 2001; Wipf and Rixen 2010; Leffler and others 2016; Niittynen and others 2020a). Observed increases in the productivity of tussock tundra may be related to variability of substrate properties including grain size and soil chemistry that are predicted to favour development of moist-acidic tundra with climate warming (Walker and others 1998; Epstein and

### Table 5. Results of the SIMPER Analysis Showing the Contribution of Species and Species Groups to Dissimilarity Among Site Types Across the Tuktoyaktuk Coastlands

| Species                | NMDS code | Percent cover | Contribution to dissimilarity (%) | Cumulative contribution (%) |
|------------------------|------------|---------------|-----------------------------------|-----------------------------|
| High greening          | Stable     |               |                                   |                             |
| Vaccinium uliginosum   | VACULI     | 0.31          | 9.80                              | 8.99                        |
| Ledum decumbens        | LEDDEC     | 23.53         | 7.12                              | 16.11                       |
| Rubus chamaemorus      | RUBCHA     | 4.81          | 7.06                              | 23.17                       |
| Betula spp.            | BETULA     | 18.49         | 6.93                              | 30.09                       |
| Salix spp.             | SALIX      | 2.74          | 5.9                               | 35.99                       |
| Arctostaphylos spp.    | ARCTO      | 1.61          | 5.79                              | 41.79                       |
| Vaccinium vitis-idaea  | VACVIT     | 23.05         | 5.4                               | 47.19                       |
| Alnus crispa           | ALNUS      | 2.19          | 5.1                               | 52.29                       |
| Lichens                | -          | 6.46          | 4.98                              | 57.27                       |
| Dryas spp.             | DRYAS      | 0.00          | 4.76                              | 62.03                       |
| Equisetum spp.         | -          | 0.02          | 4.62                              | 66.65                       |
| Petasites frigidus     | -          | 3.14          | 4.5                               | 71.15                       |
| Graminoids             | -          | 10.47         | 3.64                              | 74.79                       |
| Empetrum nigrum        | -          | 11.55         | 3.3                               | 78.09                       |
| Bryophytes             | -          | 16.12         | 3.26                              | 81.36                       |

The table shows the species and species groups accounting for 80% of the total dissimilarity and is ranked by the contribution to dissimilarity. The site type showing higher cover for a given species is shown in bold. The NMDS Code column lists the abbreviations used in Figure 7. This analysis was not completed for the Yukon North Slope because there were no differences in community composition among sites.

Figure 8. Changes in the area of selected land cover classes between 1984 and 2014 across the Yukon North Slope (green), Tuktoyaktuk Coastlands (blue), and both regions combined (red) measured using supervised classifications from Wang and others (2019).
and others 2004a; Epstein and others 2012). The tussock growth form of species such as Eriophorum vaginatum is also highly conducive to growth in nutrient poor environments through nutrient cycling within tussocks (Cholewa and Griffith 2004) and growth of deeper roots (Chapin and others 1988). Our results are also consistent with a number of studies linking tundra greening with productive cover types (Jia and others 2006; McManus and others 2012; Frost and others 2014; Campbell and others 2021; Chen and others 2021) and shrub proliferation in the low Arctic in particular (Tape and others 2006; Ropars and Bourdreaux 2012; Lantz and others 2013; Frost and others 2014; Moffat and others 2016). Our comparisons of land cover over time also show that the proportion of shrub and tussock tundra have increased since 1984 in our study regions. Higher cover of shrubby vegetation types in the Tuktoyaktuk Coastlands likely drove differences in the extent and distribution of greening between regions. Past research in this region has also shown an association between gains in shrub and herbaceous cover and increases in NDVI (Wang and Friedl 2019). The Yukon North Slope has experienced less of a transition to shrub tundra than the Tuktoyaktuk Coastlands (Figure 8) with greater overall similarity in community composition across the region (Figure 7) and we attribute the difference in the extent of observed greening between these two regions (Table 2) to differences in the intensity of shrub proliferation.

Average annual and summer temperatures across the Beaufort Delta region have increased by 3.5°C and 1.9°C, respectively, between 1926 and 2019 (Travers-Smith and Lantz 2020) with largely homogenous warming across the region (Vincent and others 2015). Widespread increases in tundra productivity are likely a response to the direct and indirect effects of this warming. Productivity responses to warming are well documented, but environmental limitations also drive differences in the response of vegetation across the Arctic (Walker and others 2006; Hudson and Henry 2009; Elmendorf and others 2012; Myers-Smith and others 2015). NDVI trends across the Arctic Coastal Plain of Alaska also show complex responses to changes in temperature and precipitation across terrain types, suggesting that climatic drivers are mediated by regional environmental factors (Lara and others 2018). Underlying climate drivers, landscape and regional variability in soils and topography are key determinants of spatial heterogeneity in vegetation responses (Raynolds and others 2008; McManus and others 2012; Lara and others 2018). This conclusion is consistent with recent studies on spatial patterns of productivity trends across northwestern North America (Chen and others 2021) and on Banks Island (Campbell and others 2021), and complements previous research highlighting terrain variability driving these regional patterns (Jia and others 2006; Tape and others 2006; Walker and others 2009; McManus and others 2012; Tape and others 2012; Berner and others 2020; Niittynen and others 2020a). Our results using EVI trends to map tundra greening are comparable to those of studies using NDVI responses; suggesting similar spatial patterns of greening (Myers-Smith and others 2020) and mechanisms driving vegetation change (Jia and others 2006; Raynolds and others 2008; McManus and others 2012). Further, EVI uses additional spectral and angular information not used by NDVI, implemented to address known issues with NDVI related to solar incidence and atmospheric conditions present (Liu and Huete 1995).

Although some researchers recommend accounting for temporal autocorrelation in time series through pre-whitening methods (Guay and others 2014; Berner and others 2020), we do not believe that this is an issue in our analyses given the temporal revisit rate of the data used and the rates of phenological development present in tundra ecosystems. Weak evidence of temporal autocorrelation of NDVI has also been documented in areas dominated by deciduous vegetation compared to evergreen vegetation due to seasonal foliage replacement and other differences in reliance on previous-year nutrient storage (Berner and others 2011). Additionally, our methods are consistent with other studies using vegetation index time series that do not implement pre-whitening procedures (Fraser and others 2014b; Nitze and Grosse 2016; Raynolds and Walker 2016; Lara and others 2018).

The Tuktoyaktuk Coastlands and Yukon North Slope provide habitat to a diversity of mammals including caribou, muskox, bears, wolves, Dall’s sheep, red fox, and wolverine (Russell and others 1993; YEWG 2004; Rickbeil and others 2018). Our observation that tussock and dwarf shrub tundra at lower elevations are most prone to increased vegetation productivity suggest that caribou who utilize this habitat type while avoiding upright shrub tundra (Russell and others 1993; Johnstone and others 2002; Rickbeil and others 2018) will be significantly impacted by ongoing vegetation change. The impacts of vegetation change on habitat use in this region should be assessed by combining landscape-scale data on vegetation change with satellite
telemetry data for caribou and other important species (see: Rickbeil and others 2018). Range expansion of moose (Tape and others 2016) and beavers (Jung and others 2016) may also be related to vegetation change and should be explored using systematic surveys and satellite telemetry.

Several recent analyses suggest that coarse resolution imagery can mute the complexities of finer-scale ecological patterns resulting in disagreement among coarse-scale remote sensing platforms (Guay and others 2014; Berner and others 2020; Myers-Smith and others 2020). Our findings show that landscape scale variation in biophysical characteristics strongly influences vegetation dynamics evident in moderate-resolution (30 m) Landsat imagery. Because tundra ecosystems exhibit heterogeneity at scales of 1–2 m (Epstein and others 2004b; Lantz and others 2010; Assmann and others 2020; Myers-Smith and others 2020), it is possible that change detection using higher-resolution sensors (such as 0.5 – 3 m resolution imagery from WorldView, QuickBird, and PlanetScope) could account for some of the unexplained variation in our models. We suggest that future research utilize high-resolution sensors calibrated to temporally contemporaneous Landsat (Markham and Helder 2012; Belward and Skøien 2015) or Sentinel-2 (Drusch and others 2012) imagery. This integration of measurements from a greater variety of remote sensing platforms and the use of Sentinel-2 imagery cross-calibrated with Landsat offers a compelling advance in remote sensing capabilities (Wulder and others 2015; Claverie and others 2018) to avail upon samples of fine scale earth observations and improve models or offer insights on the nature of local vegetation heterogeneity.

Recent work using remotely piloted aircraft systems (RPAS; or drones) also emphasizes the influence of fine-scale variability in topography on the composition and productivity of tundra plant communities (Assmann and others 2020; Cunliffe and others 2020; Myers-Smith and others 2020). Increased affordability of RPAS systems has facilitated the collection of higher spatial resolution data representing increasingly large areas and future research can take advantage of these tools to monitor changes at fine scales (Fraser and others 2016; Assmann and others 2020; Cunliffe and others 2020). We encourage the use of RPAS surveying under standardized flight and recording protocols, such as through the High Latitude Drone Ecology Network (HiLDEN; https://arcticdrones.org), to address this gap in spatial data. These data can help further explain the complex interactions between vegetation and environmental and climatic influences across spatial scales while covering greater area than is possible with ground surveys. Vegetation indices derived from satellite imagery (such as EVI or NDVI) may be influenced by factors altering surface reflectance like standing water or vegetative stress (Roy 1989; Ollinger 2011). Higher resolution imagery will make it possible to assess the influence of soil moisture, physiological stress, and disease on vegetation indices.

**CONCLUSIONS**

Global climate change is driving rapid increases in vegetation productivity across northern latitudes. The spatial heterogeneity in productivity trends highlighted in this study is the result of finer-scale, landscape processes that mediate the effects of regional climate warming. Surficial geology and topography are among the best predictors of spatial pattern in tundra greening because they influence soil conditions and moisture. Vegetation type also strongly influences changes in productivity because deciduous shrubs can respond rapidly to changes in moisture, nutrients, and temperature. Tundra vegetation change will impact wildlife habitat (Rickbeil and others 2018), surface energy balance, and carbon storage (McGuire and others 2006; Schaefer and others 2014) and understanding the drivers of landscape scale variation in vegetation shifts is critical to accurately characterize these relationships. We encourage continued research using random forests modelling to identify the role of regional processes as they relate to broader environmental change across spatial and temporal scales.

**ACKNOWLEDGEMENTS**

The authors would like to express thanks and gratitude to the Inuvialuit for allowing us to conduct this research on their lands. Funding and logistics for this research were provided by the Natural Sciences and Engineering Research Council of Canada (Discovery Grant (06210-2018) to TCL and a Canada Graduate Scholarship Award to JHS), the Northern Scientific Training Program, the Polar Continental Shelf Program, the Arctic Institute of North America, the Aurora Research Institute, and the University of Victoria. Soil processing and chemical analysis were completed at the Pacific Forestry Centre (Natural Resources Canada) in Victoria, BC. Data processing and analysis were enabled by the computational capabilities provided by Compute Canada (www.computecanada.ca).
and WestGrid (www.westgrid.ca). We would also like to thank the Aklavik Hunters and Trapper Committee, Michelle Gruben, Dennis Arey, Kiyo Campbell, Tracey Proverbs, Angel Chen, Nicola Shipman, Zander Chila, and Hana Travers-Smith for their assistance in the field and for their valuable insight and discussions on these topics. We would also like to thank two anonymous reviewers whose insightful comments helped improve this manuscript.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

OPEN ACCESS

This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

REFERENCES

Ackerman D, Griffin D, Hobbie SE, Finlay JC. 2017. Arctic shrub growth trajectories differ across soil moisture levels. Global Change Biology 23:4294–4302.

Alunik I, Morrison DA. 2003. Across time and tundra: The Inuvialuit of the Western Arctic: Raincoast Books.

Arctic Monitoring and Assessment Programme. 2004. Impacts of a Warming Arctic: Arctic Climate Impact Assessment. Cambridge, UK: Cambridge University Press.

Assmann JJ, Myers-Smith IH, Kerby JT, Cunliffe AM, Daskalova GN. 2020. Drone data reveal heterogeneity in tundra greenness and phenology not captured by satellites. Environmental Research Letters 15:125002.

Belward AS, Skøien JO. 2015. Who launched what, when and why; trends in global land-cover observation capacity from civilian earth observation satellites. Journal of Photogrammetry and Remote Sensing 103:115–128.

Berner LT, Beck PSA, Bunn AG, Lloyd AH, Goetz SJ. 2011. High-latitude tree growth and satellite vegetation indices: Correlations and trends in Russia and Canada (1982–2008).

Berner LT, Massey R, Jantz P, Forbes BC, Macias-Fauria M, Myers-Smith I, Kumpula T, Gauthier G, Andreeu-Hayles L, Gaglioti BV. 2020. Summer warming explains widespread but not uniform greening in the Arctic tundra biome. Nature Communications 11:1–12.

Bhattacharyya US, Walker DA, Raynolds MK, Comiso JC, Epstein HE, Jia G, Gens R, Pinzon JE, Tucker CJ, Tweedie CE. 2010. Circumpolar Arctic tundra vegetation change is linked to sea ice decline. Earth Interactions 14:1–20.

Bjorkman AD, Criado MG, Myers-Smith IH, Rovolainen V, Jónsdóttir IS, Westergaard KB, Lawler JP, Aronsson M, Bennett B, Gardfjell H. 2020. Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring. Ambio 49:678–692.

Bjorkman AD, Myers-Smith IH, Elmendorf SC, Normand S, Rüger N, Beck PS, Blach-Overgaard A, Blok D, Cornelissen JHC, Forbes BC. 2018. Plant functional trait change across a warming tundra biome. Nature 562:57–62.

Bonan GB, Levin S, Sitch S, Vertenstein M, Oleson KW. 2003. A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. Global Change Biology 9:1543–1566.

Bonney MT, Danby RK, Treitz PM. 2018. Landscape variability of vegetation change across the forest to tundra transition of central Canada. Remote Sensing of Environment 217:18–29.

Brady NC, Weil RR. 1996. The Nature and Properties of Soils: Prentice Hall.

Breiman L. 2001. Random forests. Machine Learning 45:5–32.

Bret-Harte MS, Shaver GR, Zoerner JP, Johnstone JF, Wagen JL, Chavez AS, Gunkelman RF IV, Lippert SC, Laundre JA. 1995. Responses of arctic tundra to experimental and observed changes in climate. Ecology 76:694–711.

Burn CR, Kokelj S. 2009. The environment and permafrost of the Mackenzie Delta area. Permafrost and Periglacial Processes 20:83–105.

Burn CR, Zhang Y. 2009. Permafrost and climate change at Herschel Island (Qikiqtaruk), Yukon Territory, Canada. Journal of Geophysical Research: Earth Surface 114:F02001.

Cameron EA, Lantz TC. 2016. Drivers of tall shrub proliferation adjacent to the Dempster Highway, Northwest Territories, Canada. Environmental Research Letters 11:045006.

Campbell TKF, Lantz TC, Fraser RH, Hogan D. 2021. High arctic vegetation change mediated by hydrological conditions. Ecosystems 24:106–121.

Chapin III, F. 1988. Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. Ecology 69:693–702.

Chaplin FS III, Shaver GR, Giblin AE, Nadelhofer KJ, Laundre JA. 1995. Responses of arctic tundra to experimental and observed changes in climate. Ecology 76:694–711.

Chen A, Lantz TC, Hermosilla T, Wulder MA. 2021. Biophysical controls of increased tundra productivity in the western Canadian Arctic. Remote Sensing of Environment 258:112358.

Cholewa E, Griffith M. 2004. The unusual vascular structure of the corn of Eriophorum vaginatum: implications for efficient retranslocation of nutrients. Journal of Experimental Botany 55:731–741.
Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143.

Claverie M, Ju J, Masek JG, Dungan JL, Vermote EF, Roger J-C, Skakun SV, Justice C. 2018. The Harmonized Landsat and Sentinel-2 surface reflectance data set. Remote Sensing of Environment 219:145–161.

Cunliffe AM, Assmann JJ, Daskalova GN, Kerby JT, Myers-Smith IH. 2020. Aboveground biomass correlates strongly with drone-derived canopy height but weakly with greenness (NDVI) in a shrub tundra landscape. Environmental Research Letters 15:125004.

Cutler DR, Edwards TC Jr, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ. 2007. Random forests for classification in ecology. Ecology 88:2783–2792.

Dagg J, Lafleur P. 2011. Vegetation community, foliar nitrogen, and temperature effects on tundra CO2 exchange across a soil moisture gradient. Arctic, Antarctic, and Alpine Research 43:189–197.

Davy R, Chen L, Hanna E. 2018. Arctic amplification metrics. International Journal of Climatology 38:4384–4394.

De'ath G. 2007. Boosted trees for ecological modeling and prediction. Ecology 88:243–251.

De Reu J, Bourgeois J, Bats M, Zwetvaegher A, Gelorini V, De Smedt P, Chu W, Antrop M, De Maeyer P, Finke P. 2013. Application of the topographic position index to heterogeneous landscapes. Geomorphology 186:39–49.

Deslippe JR, Hartmann M, Simard SW, Mohn WW. 2012. Long-term warming alters the composition of Arctic soil microbial communities. FEMS Microbiology Ecology 82:303–315.

Deslippe JR, Simard SW. 2011. Below-ground carbon transfer among Betula nana may increase with warming in Arctic tundra. New Phytologist 192:689–698.

Drusch M, Del Bello U, Carlier S, Colin O, Fernandez V, Gascon F, Hoersch B, Isola C, Laberinti P, Martinotti P. 2012. Sentinel-2: ESA’s optical high-resolution mission for GMES operational services. Remote Sensing of Environment 120:25–36.

Duk-Rodkin A, Hughes OL. 1995. Quaternary geology of the northern part of the central Mackenzie Valley corridor, District of Mackenzie, Northwest Territories: Geological Survey of Canada.

Ecosystem Classification Group. 2012. Ecological Regions of the Northwest Territories, Southern Arctic, Yellowknife, NT, p170.

Elmendorf SC, Henry GH, Hollister RD, Bjork RG, Boulanger-Lapointe N, Cooper EJ, Cornelissen JH, Day TA, Dorrepaal E, Elumeeva TG. 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change 2:453–457.

Environment and Climate Change Canada. 2018a. Canadian climate normals 1981–2010 station data. Tuktoyaktuk A. Ottawa, Ontario.

Environment and Climate Change Canada. 2018b. Canadian climate normals 1981–2010 station data. Shingle Point A. Ottawa, Ontario.

Epstein HE, Beringer J, Gould WA, Lloyd AH, Thompson C, Chapin FS III, Michaelson GJ, Ping CL, Rupp T, Walker DA. 2004a. The nature of spatial transitions in the Arctic. Journal of Biogeography 31:1917–1933.

Epstein HE, Calef MP, Walker MD, Chapin FS III, Starfield AM. 2004b. Detecting changes in arctic tundra plant communities in response to warming over decadal time scales. Global Change Biology 10:1325–1334.

Epstein HE, Raynolds MK, Walker DA, Bhatt US, Tucker CJ, Pinzon JE. 2012. Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. Environmental Research Letters 7:015506.

Evans J. 2020. spatialEco: R package version 1.3–0.

Fraser RH, Lantz TC, Olthof I, Kokelj SV, Sims RA. 2014a. Warming-induced shrub expansion and lichen decline in the Western Canadian Arctic. Ecosystems 17:1151–1168.

Fraser RH, Olthof I, Kokelj SV, Lantz TC, Lachelle D, Brooker A, Wolfe S, Schwarz S. 2014b. Detecting Landscape Changes in High Latitude Environments Using Landsat Trend Analysis: 1. Visualization. 6:11533–11557.

Fraser RH, Olthof I, Lantz TC, Schmitt C. 2016. UAV photogrammetry for mapping vegetation in the low-Arctic. Arctic Science 2:79–102.

Friedman JH. 2001. Greedy function approximation: a gradient boosting machine. Annals of Statistics. 29:1189–1232.

Frost GV, Epstein HE, Walker DA. 2014. Regional and landscape-scale variability of Landsat-observed vegetation dynamics in northwest Siberian tundra. Environmental Research Letters 9:025004.

Fulton RJ. 1989. Quaternary geology of Canada and Greenland. Ottawa, Ontario: Geological Survey of Canada.

Gamon JA, Huenefrikh RF, Stone RS, Tweddie CE. 2013. Spatial and temporal variation in primary productivity (NDVI) of coastal Alaskan tundra: Decreased vegetation growth following earlier snowmelt. Remote Sensing of Environment 129:144–153.

Gao X, Huete AR, Ni W, Miura T. 2000. Optical–biophysical relationships of vegetation spectra without background contamination. Remote Sensing of Environment 74:609–620.

Gill D. 1972. The point bar environment in the Mackenzie River Delta. Canadian Journal of Earth Sciences 9:1382–1393.

Gill D. 1973. Floristics of a plant succession sequence in the Mackenzie Delta, Northwest Territories. Polarforschung 43:55–65.

Guay KC, Beck PS, Berner LT, Goetz SJ, Baccini A, Buermann W. 2014. Vegetation productivity patterns at high northern latitudes: A multi-sensor satellite data assessment. Global Change Biology 20:3147–3158.

Hastie T, Tibshirani R, Friedman J. 2009. The elements of statistical learning: data mining, inference, and prediction: Springer Science & Business Media.

Hermosilla T, Wulder MA, White JC, Coops NC, Hobart GW, Campbell LB. 2016. Mass data processing of time series Landsat imagery: pixels to data products for forest monitoring. International Journal of Digital Earth 9:1035–1054.

Hijmans RJ. 2020. raster: geographic data analysis and modeling: R package version 3.0–12.

Hobbie SE, Chapin FS III. 1998. The response of tundra plant biomass, aboveground production, nitrogen, and CO2 flux to experimental warming. Ecology 79:1526–1544.

Hudson JM, Henry GH. 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology 90:2657–2663.

Hughes O, Harington CR, Janssens J, Matthews Jr J, Morlan RE, Rutter N, Schweger CE. 1981. Upper Pleistocene stratigraphy, paleoecology, and archaeology of the northern Yukon interior, eastern Beringia 1. Bonnet Plume Basin. Arctic: 329–365.

Jessop AM. 1971. The distribution of glacial perturbation of heat flow in Canada. Canadian Journal of Earth Sciences 8:162–166.
Walker MD, Wahren CH, Hollister RD, Henry GH, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carroll AB. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences 103:1342–1346.

Wang J, Sulla-Menashe D, Woodcock CE, Sonnentag O, Keeling R, Friedl M. 2019. ABoVE: Landsat-derived Annual Dominant Land Cover Across ABoVE Core Domain, 1984–2014. Oak Ridge, Tennessee, USA: ORNL DAAC.

Wang JA, Friedl MA. 2019. The role of land cover change in Arctic-Boreal greening and browning trends. Environmental Research Letters 14:125007.

Wiedmer E, Senn-Irlet B. 2006. Biomass and primary productivity of an Alnus viridis stand—a case study from the Schächental valley, Switzerland. Botanica Helvetica 116:55–64.

Wipf S, Rixen C. 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. Polar Research 29:95–109.

Wulder MA, Hilker T, White JC, Coops NC, Masek JG, Pfugmacher D, Crevier Y. 2015. Virtual constellations for global terrestrial monitoring. Remote Sensing of Environment 170:62–76.

Wulder MA, Loveland TR, Roy DP, Crawford CJ, Masek JG, Woodcock CE, Allen RG, Anderson MC, Belward AS, Cohen WB. 2019. Current status of Landsat program, science, and applications. Remote Sensing of Environment 225:127–147.

Yukon Ecoregions Working Group. 2004. Ecoregions of the Yukon Territory: Biophysical properties of Yukon landscapes. PARC Technical Bulletin, p63–72.