THE UNIVERSITY of EDINBURGH

Edinburgh Research Explorer

Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change

Citation for published version:
Myers-Smith, I, Grabowski, MM, Thomas, H, Angers-blondin, S, Daskalova, GN, Bjorkman, A, Cunliffe, AM, Assmann, JJ, Boyle, J, McLeod, E, McLeod, S, Joe, R, Lennie, P, Arey, D, Gordon, R & Eckhert, C 2019, 'Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change' Ecological Monographs, vol. 87, no. 2. DOI: 10.1002/ecm.1351

Digital Object Identifier (DOI):
10.1002/ecm.1351

Link:
Link to publication record in Edinburgh Research Explorer

Document Version:
Peer reviewed version

Published In:
Ecological Monographs

General rights
Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.

Download date: 21. Jun. 2019

Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change

Isla H. Myers-Smith[1], Meagan M. Grabowski[2], Haydn J.D. Thomas[1], Sandra Angers-Blondin[1], Gergana N. Daskalova[1], Anne D. Bjorkman[1,3], Andrew M. Cunliffe[1], Jakob J. Assmann[1], Joseph Boyle[1], Edward McLeod[4,5], Samuel McLeod[4,5], Ricky Joe[4,5], Paden Lennie[4,5], Deon Arey[4,5], Richard Gordon[4,6], Cameron Eckert[4]*

1. School of GeoSciences, University of Edinburgh, Edinburgh, UK
2. Whitehorse, Yukon, Canada
3. Department of Bioscience, Aarhus University, Denmark
4. Yukon Parks, Department of Environment, Yukon Territorial Government, YT, Canada
5. Aklavik, Northwest Territories, Canada
6. Inuvik, Northwest Territories, Canada

*Corresponding author: Isla H. Myers-Smith, isla.myers-smith@ed.ac.uk

Keywords:
tundra, greening, phenology, community composition, growth, climate change, warming, permafrost

Abstract

The Arctic tundra is warming rapidly, yet the exact mechanisms linking warming and observed ecological changes are often unclear. Understanding mechanisms of change requires long-term monitoring of multiple ecological parameters. Here, we present the findings of a collaboration between government scientists, local people, park rangers and academic researchers that provide insights into

changes in plant composition, phenology and growth over 18 years on Qikiqtaruk–Herschel Island, Canada. Qikiqtaruk is an important focal research site located at the latitudinal tall shrub line in the western Arctic. This unique ecological monitoring program indicates the following findings: 1) nine days per decade advance of spring phenology, 2) a doubling of average plant canopy height per decade, but no directional change in shrub radial growth and 3) a doubling of shrub and graminoid abundance and a decrease by half in bare ground cover per decade. Ecological changes are concurrent with satellite-observed greening and when integrated suggest that indirect warming from increased growing season length and active layer depths, rather than warming summer air temperatures alone, could be important drivers of the observed tundra vegetation change. Our results highlight the vital role that long-term and multi-parameter ecological monitoring plays in both the detection and attribution of global change.

Introduction

Arctic tundra is responding rapidly to climate change (IPCC 2014). Annual temperatures in the Arctic have already increased by more than 2°C since 1978 (IPCC 2013) and there is growing evidence that this warming is leading to changes in vegetation communities at sites around the tundra biome (Myers-Smith et al. 2011a, Elmendorf et al. 2012b, IPCC 2014). Although the literature reports prominent ecological transformations, including changes in vegetation composition (Elmendorf et al. 2012b), plant phenology, and satellite-observed greening (Post et al. 2009a), recent studies also indicate high unexplained heterogeneity in vegetation responses at sites around the Arctic (Elmendorf et al. 2012b, Oberbauer et al. 2013, Guay et al. 2014, Myers-Smith et al. 2015a, Prevéy et al. 2017). One possible reason that tundra biome-scale data syntheses indicate high levels of heterogeneity is that different ecological parameters are measured in different places or at different points in time. Rarely are single sites monitored to a degree at which we can observe patterns of change over time from multiple lines of evidence (Hobbie et al. 2017). This omission also often precludes exploration of the potential mechanistic drivers of observed change. Thus, to understand the trends and drivers of change in tundra ecosystems, we require integrated assessments of multiple and concurrently monitored ecological parameters at focal research sites.

Widely-observed ecological patterns

Vegetation monitoring indicates an increase in total plant cover and decrease in bare ground in tundra ecosystems (Elmendorf et al. 2012b). Tundra plant community composition change indicates a shift towards increased deciduous shrub cover – shrub expansion (Myers-Smith et al. 2011a) and graminoid cover (Elmendorf et al. 2012b), while mosses and lichen species tend to be decreasing (Lang et al. 2012, Elmendorf et al. 2012b). The same changes have been observed in warming experiments (Walker et al. 2006, Elmendorf et al. 2012a), suggesting that these vegetation changes are driven at least in part

by increasing temperatures (Elmendorf et al. 2015). Shrub and graminoid plants are also growing taller (Walker et al. 2006, Myers-Smith et al. 2011c) and reproducing more frequently (Klady et al. 2011). However, rates of shrub expansion vary greatly across sites, with some showing no evidence of change or climate sensitivity of growth (Hudson and Henry 2010, Myers-Smith et al. 2011b, 2015a, Elmendorf et al. 2012b, Martin et al. 2017, Isla H. and David S. 2017). Heterogeneity in vegetation change can be explained by a variety of site-level factors including soil moisture (Ackerman et al. 2017), topography (Tape et al. 2012, Ropars and Boudreau 2012), disturbance (Lantz et al. 2009, 2010), herbivory (Olofsson et al. 2009, Zamin and Grogan 2012), and plant-plant interactions (Bret-Harte et al. 2004, Dormann et al. 2004).

Increasing temperatures are widely expected to lead to advances in plant phenological events including leaf emergence and flowering (Peñuelas and Filella 2001, Peñuelas et al. 2009, Körner and Basler 2010, Pau et al. 2011, Cleland et al. 2012). In tundra ecosystems, the timing of leaf emergence and flowering has advanced at some (Høye et al. 2007, Kerby and Post 2013, Iler et al. 2013), but not all sites (Bjorkman et al. 2015b). Satellite-observed green-up in the tundra is estimated to be advancing by 1.6 to 4.7 days per decade (Myneni et al. 1997, Zeng et al. 2011, Park et al. 2016), corresponding with an advance in snow melt (Post et al. 2009b) and increased spring drawdown of CO_2 in the northern hemisphere (Barichivich et al. 2013, Forkel et al. 2016). However, growing season onset varies greatly by region and different remotely-sensed satellite records (Zeng et al. 2011, Xu et al. 2013), and some tundra sites have experienced decreased growing season length and delayed phenology as a result of higher snowfall (Wipf and Rixen 2010, Bjorkman et al. 2015a, Legault and Cusa 2015).

Satellite observations indicate a greening of Arctic tundra concurrent with recent warming that has been attributed to an increase in photosynthetic biomass (Jia et al. 2009, Forbes et al. 2010, Beck and

Goetz 2011, Bhatt et al. 2013, Ju and Masek 2016). However, recent studies indicate a decrease in the satellite greening trend (Bhatt et al. 2013) and heterogeneity in satellite observations across different sensor platforms (Guay et al. 2014). Non-ecological factors, including atmospheric change, drift in satellite sensors or earlier snow melt, can also produce greening signals (Gamon et al. 2013, Guay et al. 2014). For example, the normalized difference vegetation index (NDVI), the most common index of remotely-sensed tundra greening, is also sensitive to other landscape-level parameters such as snow duration or standing water (Gamon et al. 2013, Raynolds et al. 2013, Pattison et al. 2015). Thus, there is current uncertainty in whether the greening patterns observed by satellites do indeed indicate a change in plants *in situ* at sites across the tundra biome.

Multi-parameter evidence of change

Comprehensive monitoring programs that incorporate environmental variables, community composition and phenology observations are rare in the Arctic, especially considering the rapid rate of environmental change and potential sensitivity of tundra ecosystems (CAFF 2013, Hobbie et al. 2017). These long-term integrated datasets are required to test the ability of remote sensing to capture *in situ* ecological change. At present, there are only a few circumpolar Arctic sites with such long-term, multi-parameter monitoring including research stations such as Abisko (68.35ºN, 18.83ºE) in Northern Sweden (Van Wijk et al. 2004, Callaghan et al. 2010, 2013, Hobbie et al. 2017), Toolik Lake (68.63ºN, -149.60ºE) in Northern Alaska (Van Wijk et al. 2004, Hobbie et al. 2017), Zackenberg (74.50ºN, -27.77ºE) in Eastern Greenland (Høye et al. 2007, Iler et al. 2013) and Alexandra Fiord (78.88ºN, -75.80ºE) on Ellesmere Island in Arctic Canada (Svoboda et al. 1994, Hudson and Henry 2009, 2010, Hudson et al. 2011, Bjorkman et al. 2015a).

The ecological monitoring program on Qikiqtaruk was established in 1999 uniquely combining multi-parameter monitoring using international protocols with the collaborative efforts of territorial park rangers, Yukon government researchers, and academic scientists (Box 1). Early outputs of the monitoring program indicated an increase in shrub cover at sites across this island (Myers-Smith et al. 2011b). Qikiqtaruk is located in a region of the Arctic that has undergone a prominent greening trend according to different satellite records (Fraser et al. 2011, Guay et al. 2014, Ju and Masek 2016), and research is under way to determine how vegetation changes align with changes in phenology and overall community structure in the context of regional increases in NDVI. After 18 years of ecological monitoring, we can now test whether the original observations of vegetation change are continuing at this site and whether rates of change in environmental and ecological parameters are accelerating.

In this study, we combine multiple ecological parameters covering a 18-year timescale (1999-2017) to test three hypotheses: 1) The realized growing season length (time between leaf emergence and leaf senescence) has increased concurrent with earlier snow melt and warmer spring and autumn temperatures; 2) The canopy height of tundra shrubs is increasing, driven by high sensitivity of interannual growth to summer temperature; 3) Vegetation community composition change is occurring with an increase in shrub and graminoid abundance concurrent with a decrease in bare ground. We place these hypotheses in the context of environmental change in the western Arctic Region to understand the mechanisms, patterns, and implications of the observed vegetation change.

Box 1. ***Collaborative Ecological Monitoring on Qikiqtaruk***

Ecological monitoring of community composition and phenology requires consistent and time-consuming observations recorded throughout the growing season. This poses major logistical challenges for researchers, and is a primary contributing factor to the scarcity of long-term Arctic

vegetation monitoring programs (CAFF 2013). Recently, the integration of local people into long-term ecological research has led to an increasing emphasis on community-based monitoring around the Arctic (Gill and Lantz 2014, Stern 2015). However, the different types of monitoring from community-based research, government-funded monitoring, and academic research are rarely integrated.

Vegetation monitoring on Qikiqtaruk incorporates collaboration among government, park rangers including local Inuvialuit people, and university-based researchers. The vegetation monitoring program was initiated on Qikiqtaruk by Yukon Government biologists in 1999 and continues today (Smith et al. 1989, Cooley et al. 2012). It is carried out by park rangers, and supplemented by government scientists and academic researchers who monitor long-term community composition plots and collect other associated ecological data. Researchers benefit by the access to long-term monitoring data and local knowledge, and in turn provide data analysis and additional protocols to enhance Yukon Parks' monitoring programs. Direct contact and collaboration takes place during the summer field season, providing valuable opportunities for the co-production of knowledge between local observations by those living in the region and working on Qikiqtaruk and those visiting to conduct scientific research.

The Qikiqtaruk monitoring program (Figure 1) has one of the highest temporal resolutions among vegetation phenology monitoring datasets collected anywhere in the Arctic (CAFF 2013). Data are collected every 2-3 days from snow melt (April) to senescence (September). This comparatively high frequency of data collection over the whole growing season enables an understanding of ecological changes in the context of local observations (Cooley et al. 2012). Data from the ecological monitoring program have previously contributed to tundra-biome wide data syntheses (Elmendorf et al. 2012b, 2015, Prevéy et al. 2017). The monitoring program is also important for communicating how climate change is influencing tundra systems in the western Arctic (Stern and Gaden 2015).

Materials and methods

Site description

Qikiqtaruk - Herschel Island is located on the Arctic Coast of the Yukon Territory (69.6°N, 138.9°W) at the northern extent of tall shrubs and in a zone of ice-rich permafrost (Figure 2). In the larger western Arctic region, there is evidence for widespread shrub expansion (Tape et al. 2006, Myers-Smith et al. 2011b, Lantz et al. 2013, Moffat et al. 2016). Qikiqtaruk is also located at the mid-Arctic latitudes where shrub vegetation has been found to be especially sensitive to climate (Myers-Smith et al. 2015a); though the climate sensitivity of shrub radial growth has been observed to be low at this particular site (Myers-Smith et al. 2011c, 2015a).

The island is made up of discrete vegetation types (Smith et al. 1989, Obu et al. 2015). The dominant vegetation types include the Herschel vegetation type: comprising relatively undisturbed moist acidic tussock tundra, the Komakuk vegetation type: comprising herbaceous and grassy tundra that is more influenced by cryoturbation and surface disturbance, the Orca vegetation type: comprising tall shrub and wet sedge vegetation across a floodplain: and other more transitional vegetation types in the areas with more topographic variation. These vegetation types have been mapped and correspond to different landscape contexts, soil conditions and disturbance histories across the island (Obu et al. 2015).

Environmental parameters

Climate data were compiled from monthly Climate Research Unit (CRU) TS3.21 gridded frost frequency data (0.5˚ resolution, Harris, Ian 2013), and the Herschel Island Environment Canada Weather station. Seasons were defined as spring: April - May, summer: June - July, autumn: August - September, winter: October - March. Sea ice data are from the Canadian Sea Ice Service for the CIA WA Beaufort Sea: Mackenzie region (CWA01_02). We report climate data from the Environment

Canada weather station (red point on Figure 2) as temperatures across the monitoring locations do not differ substantially across these relatively flat upland or floodplain locations (IH Myers-Smith and HJD Thomas, unpublished data). Snow melt, soil temperature and active layer data are measure at the plot-level (see below).

Active layer depth was measured by vertically probing the soil using a metal stake and measuring the depth to frozen ground. Records from 1985 come from the ecological surveys prior to the establishment of Herschel Island – Qikiqtaruk Territorial Park (Smith et al. 1989). Records from 2003 – 2008 come from previous studies by Prof. Chris Burn (Burn and Zhang 2009) and the ArcticWOLVES project (http://www.cen.ulaval.ca/arcticwolves/en_intro.htm, S Gilbert, D Reid, CJ Krebs and IH Myers-Smith, unpublished data). Records from 2016 – 2017 come from the NERC ShrubTundra project and a new active layer monitoring protocol developed in 2017 to accompany the species composition and phenology data collection.

Soil temperature was measured monthly from April to September at different depths, ranging from 1 m to 42 m below the surface, at two borehole stations (15 m depth: 2000 - 2017 and 43 m depth: 2005 - 2017). The boreholes are located within 20 m of each other on a flat surface on Collinson Head on Qikiqtaruk and are equipped with BetaTHERM 2.2K3A1A thermistors, which were calibrated in a laboratory ice bath. Park rangers recorded resistance in the circuit using a multimeter, calibrated against a stable resistor of 7355 W before each set of measurements. Resistance values (Ω) were converted into temperature (°C) following (Burn and Zhang 2009), see Table S1 for formulas. We present minimum soil temperatures from 12, 15 and 16 m depths across the time series as these were the depths at which there were the most available data.

Vegetation phenology

Vegetation phenology methodology follows the ITEX protocols (Molau and Mølgaard 1996) and includes three monitored species: *Dryas integrifolia* Vahl*, Eriophorum vaginatum* L.*,* and *Salix arctica* Pall. For each species, one transect, with 10 individuals, stems or plots per 50 m transect, is marked by wooden stakes. The first species, *Dryas integrifolia* (Mountain Avens), is a small prostrate-growing evergreen dwarf shrub with white flowers (Figure 1 - center top). Individuals are demarcated by 10 quadrats (10 cm by 10 cm). The second species, *Eriophorum vaginatum* (Cottongrass), is a tussock grass that has large cotton-like seed heads (Figure 1 - center middle). Individuals are ten marked tussocks in a row. The third species, *Salix arctica* (Arctic Willow), is a prostrate-growing deciduous dwarf shrub with oblong leaves and large catkins (Figure 1 - center bottom). Individuals were initially marked by stem tags, but due to continued stem mortality this changed during 2015 to quadrats similar to the *Dryas integrifolia* transect. Phenology variables observed are indicated in Figure 1. Realized growing season length was estimated as the difference between the first leaf emergence date and the first leaf senescence date (P5-P2). We used first leaf senescence (P5) to represent the end of growing season due to a lack of last leaf senescence (P6) data in some years.

Dendroecology methods

Annual growth increments in woody species provide information on growth and climate sensitivity, particularly when no long-term monitoring data are available. Wood samples of deciduous willow species *Salix arctica*, *S. pulchra* Cham., *S. richardsonii* Hook., *S. glauca* L and *S. niphoclada* Rydberg. were collected in 2009 and 2015 (Myers-Smith et al. 2011c, 2015a), S Angers-Blondin and IH Myers-Smith, unpublished data). Wood processing followed methods adapted for tundra shrub species (Myers-Smith et al. 2015b). Thin cross sections of either the largest stem or the root collar were mounted on glass slides and photographed under a dissecting microscope. Rings were counted and

measured from the digital image for each shrub section along four radii with a resolution of 1 µm (Schneider et al. 2012). Temporal growth trends in raw ring width are presented here to complement ecological monitoring data, and to test whether secondary growth follows the same trends as primary growth.

Community composition

Community composition was measured in two vegetation communities (Figure 1): the Herschel vegetation type and the Komakuk vegetation type. Community composition was assessed using point-framing methods following the ITEX protocols (Molau and Mølgaard 1996). Twelve plots of 1 m^2 (six per vegetation type) were established in 1999 and resurveyed in 2004, 2009 and 2013 - 2017. A grid with 100 points at 10 cm spacing was placed over each plot at a height of approximately 50 cm. A metal pin was dropped vertically at each of the 100 grid points; all plant parts that touched the pin were recorded, noting species, plant part (leaf, stem, flower, flower stalk) and tissue status (live or dead). The maximum canopy height at each point and the height of the tall shrub species *Salix pulchra* were also recorded at every grid point. Soil surface cover was recorded including bare ground, rock, litter, moss, and lichen species. Species counts and bare ground were converted to abundance by calculating the proportion of points at which each species was present. Plant cover was represented using a vegetation cover index calculated by dividing the total number of vegetation hits per plot by the number of points per plot (100), such that a vegetation index of one would represent an average of one hit per sample point.

We measured the number of species adjacent to the species composition monitoring plots following the 2017 International Tundra Experiment species pool monitoring protocol (C. Rixen, https://www.gvsu.edu/itex/). A survey of the local species pool within 100 m of the community

composition plots was conducted on 31st July and 1st August of 2017. We monitored a 50 by 50 cm plot within the central monitoring plot at each vegetation type, a 1 by 1 m plot (the central monitoring plot), a 2.5 m radius circular plot centred around the monitoring plot, and then walked concentric circles out to 100 m spaced approximately 5 m apart, recording all plant species observed and their distance to the center plot. These data were used to make species area curves to test the proximity of new species that could potentially occur in the monitoring plots in future.

Statistical analyses

Statistics were conducted with the software R (version 3.3.3, R Core Team 2014). Bayesian models were conducted in the package MCMCglmm (Hadfield 2010) except for the interval censoring models that were written in JAGS called from R using the programs rjags (Plummer 2014) and R2jags (Su and Yajima 2012). Convergence was assessed through examination of trace plots and autocorrelation values, and in the case of the interval censoring models using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) available in the coda package (Plummer et al. 2006). Code is available at the following GitHub repository (link to be added at the time of publication).

We used Bayesian linear models to estimate change in seasonal temperature, frost frequency days, snow melt date and active layer depth. We used Bayesian linear models to estimate changes in minimum soil temperature (square transformed) at depths of 12, 15 and 16 m in different years in two boreholes located near the community composition plots. We used a Bayesian model with a binomial distribution to estimate change in minimum sea ice concentration over time as sea ice concentration is bounded between 0 and 1. We used hierarchical Bayesian linear interval censoring models with plot and year as random effects to estimate change in phenology over time to account for the uncertainty in the timing of the phenological event between monitoring observations (Bjorkman et al. 2015a). We

used hierarchical Bayesian models with plot and year as random effects to estimate change in overall canopy height, *Salix pulchra* height (Gaussian distribution), and change in vegetation cover, bare ground cover and species evenness (binomial distribution) over time as percent cover data are bounded between 0 and 1. We used four hierarchical Bayesian linear models with individual and year as random effects to estimate change in radial growth over time for the willow species *Salix arctica*, *S. pulchra*, *S. richardsonii*, and *S. glauca*. We estimated species richness at the site level (aggregated species richness across all plots) over time using a Bayesian linear model, as the hierarchical model would not converge. We used Bayesian linear models to estimate accumulation of species at different distances (log transformed) in the Herschel and Komakuk vegetation types. We used non-informative parameter-expanded priors for all coefficients in the MCMCglmm models that included random effects, and non-informative priors for all coefficients in the JAGS models. We used a uniform prior between 0 and 365 for the intercepts and slope priors were normally distributed, centered on zero with a precision of 0.001. We refer to predictors as 'significant' when the 95% credible interval for the corresponding parameter in the fitted models did not overlap zero.

Results

Observed climate and environmental climate change

Over the past 25 years Qikiqtaruk has experienced warming towards the end of the ice-free season (August and September) and a decrease in the annual number of frost days (inversely related to potential growing season length) by 3.6 days per decade (slope = -0.36, CI = -0.58 to -0.12, $p < 0.01$), and warming during the growing season (slope = 0.16, CI = 0.01 to 0.31, $p = 0.04$, Figure 3b). Minimum sea ice concentration has also declined over the same period (slope = -0.11, CI = -0.17 to -0.05, $p < 0.01$) and the day that snow is completely melted at plots along the phenology transects is occurring earlier (slope = -0.71, CI = -1.37 to -0.05, $p = 0.04$). Minimum soil temperatures at 12, 15

and 16 m depths have increased across the monitoring period at both boreholes (slope = 0.004, CI = 0.003 to 0.005, $p < 0.01$ for soil temperature at 12 m depth in the first borehole, see Table S2 for all model outputs).

Data from different datasets in the Herschel and Komakuk vegetation types monitored within 1 km of the ecological monitoring sites from 1985 and 2017 indicate a mean increase in the active layer depth by as much as 20 cm (slope = 0.72, CI = 0.21 to 1.29, $p = 0.02$, Figure 4a). During the 2017 growing season, the active layer depth reached maximum depths of 58.5 cm in the Herschel vegetation type and 87.2 cm in the Komakuk vegetation type (Figure 4b).

Observed vegetation change

Vegetation change appears to be progressing rapidly in certain locations including across the floodplain vegetation type (Orca vegetation type) on Qikiqtaruk as indicated by the increase in shrub cover and height in the repeat photography time series across the monitoring period (Figure 5).

a. Plant phenology

The timing of spring events has advanced for all species. *Salix arctica* leaf emergence has advanced by approximately nine days per decade (slope = -0.93, CI = -1.69 to -0.12) and flowering has advanced by approximately five to eight days per decade for all monitored species (Figure 6, Table S2). Realized growing season length (the difference between spring leaf emergence and autumn senescence for *Salix arctica*) has increased slightly by approximately two days per decade (slope = 0.21, CI = -0.92 to 1.36); this is largely due to an advance in spring phenology (leaf emergence), since leaf senescence also advanced by seven days per decade (slope = -0.74, CI = -1.53 to 0.03; Figure 6). However, only the

advance in leaf emergence was significant (the credible interval on slope estimate does not overlap zero).

b. Plant growth

Mean canopy height has more than tripled from 3.8 to 16.8 cm in the Herschel plots (slope = 0.59, CI = 0.42 to 0.79, $p < 0.01$) and from 1.6 to 11.3 cm in the Komakuk plots (slope = 0.31, CI = 0.20 to 0.43, $p < 0.01$) over the monitoring period (Figure 7a). This increase in community-level plant height is explained by both changing composition, notably an increase in taller graminoid species, and by an increase in individual species such as *Salix pulchra* canopy height over time (Figure 7b). The radial growth of *Salix* spp. showed large inter-annual variability and no clear annual trend or climate sensitivity (Figure 7c).

c. Community composition

Repeat vegetation monitoring has identified changes to the overall structure of communities and directional changes in community composition (Figure 8). Plant cover (Figure 8a) has increased in both vegetation types since 1999, by 0.26 hits per point per year (slope = 0.26, CI = 0.09 to 0.42, $p = 0.01$) for the Herschel vegetation type and 0.11 hits per year (slope = 0.11, CI = 0.03 to 0.19, $p = 0.02$) for the Komakuk vegetation type. Increasing vegetation cover is associated with a decrease in bare ground (Herschel vegetation type: slope = -0.18, CI = -0.35 to -0.02, $p = 0.02$; Komakuk vegetation type: slope = -0.07, CI = -0.13 to 0.00, $p = 0.06$, Figure 8b) and an increase in canopy height (Figure 7a). Species richness and species evenness have not changed over time (Figure 8c and d, Table S2). In the Herschel plots, there was an increase in *Eriophorum vaginatum* (slope = 0.10, CI = -0.03 to 0.23, $p = 0.12$; Figure 8e) and *Salix pulchra* cover (slope = 0.06, CI = -0.02 to 0.14, $p = 0.11$; Figure 8e). Finally, two graminoid species, *Arctagrostis latifolia* and *Alopecurus alpinus*, have immigrated into the Komakuk

vegetation plots and expanded their cover over the last decade (*Arctagrostis latifolia*: slope = 0.20, CI = -0.01 to 0.41, p = 0.06; *Alopecurus alpinus*: slope = 1.50, CI = 0.64 to 2.61, p <0.01, Figure 8f).

We found faster accumulation of species in the Herschel vegetation type (slope = 6.50, CI = 5.70 to 7.32, p < 0.01) relative to the Komakuk vegetation (slope = 8.61, CI = 7.53 to 9.72, p < 0.01, Figure 9). There were 13 vascular plant species within 100 m of the Herschel vegetation type and 26 within 100 m of the Komakuk vegetation type that have not yet been observed in the long-term monitoring plots. We have observed one species invasion into the plots the grass *Alopecurus alpinus* and one major change in abundance the grass *Arctagrostis latifolia* over the monitoring period (Figure 8).

Discussion

Observed vegetation change

Our results provide strong evidence for multi-dimensional vegetation change on Qikiqtaruk across the period 1999 to 2017 (Figure 10). We find that plant phenology, growth and community composition are changing on the island, with earlier leaf emergence, an increase in shrub canopy heights, and increased cover of shrub and graminoid species concurrent with a decrease in the cover of bare ground (Figures 5-8). These results are consistent with the initial findings reported for this site (Myers-Smith et al. 2011b) and indicate that vegetation changes have continued or accelerated over the 18-year period. Our results also correspond with widespread observations of phenology change (Ellebjerg et al. 2008, Oberbauer et al. 2013), community composition change (Elmendorf et al. 2012b, 2015) and shrub expansion across the tundra biome (Tape et al. 2006, Forbes et al. 2010, Naito and Cairns 2011, Myers-Smith et al. 2011a, Martin et al. 2017) and with predictions from tundra warming experiments (Walker et al. 2006, Elmendorf et al. 2012b, 2015). However, our results are unique because the different lines of evidence for vegetation change reported in this study come from the same or adjacent vegetation

communities and can be compared directly to concurrent changes in environmental parameters (Figure 10).

Spring phenology advanced for all three monitored species (*Salix arctica*, *Dryas integrifolia* and *Eriophorum vaginatum*), though these trends were weak due to high inter-annual variation (Figure 6). Our results also suggest that date of snow melt is a key control on spring phenology in tundra ecosystems, with earlier snow melt corresponding with earlier leaf emergence (Figures 3 and 6). Similarly, declining sea ice has also been associated with spring greening in a number of studies (Bhatt et al. 2010, Kerby and Post 2013, Post et al. 2016), which has also been observed at this site. In contrast, some studies have identified trends towards later phenology in some species and locations usually aligning with later snow melt (Schmidt et al. 2006, Wipf and Rixen 2010, Bjorkman et al. 2015a).

Our findings indicate that the length of the realized growing season on Qikiqtaruk has not substantially increased due to both an advance in leaf emergence and senescence for the species *Salix arctica* (Figure 6). This result could indicate a fixed leaf life span in the species *Salix arctica* as observed in deciduous tree species (Keenan and Richardson 2015). Lack of change in realized growing season length contrasts with the observed increase in the potential growing season length (as estimated from the number of frost days; four days per decade). This is likely due to the importance of snow melt, rather than spring temperature, in determining the start of the growing season at this Arctic tundra site (Høye et al. 2007, Oberbauer et al. 2013, Bjorkman et al. 2015a) and the lack of correspondence among trends of autumn warming and end of season phenology (Figures 3 and 6). Our findings align with previous work that suggests photoperiod (Arft et al. 1999, Andrews et al. 2011) or deterministic leaf age (Oberbauer et al. 2013) could be more influential for the timing of senescence than temperature.

Plant canopy heights have increased across the period of monitoring (Figure 7), driven by both community composition change and plastic responses in existing individuals. We observed greater variation in *Salix pulchra* canopy heights in recent years, though this is most likely driven by increased abundance of this species. Data collection has mostly been carried out by the same observers from 2009 to 2017 for both the plant cover and phenology datasets, suggesting minimal changes in observer bias across this period. An increase in both community and species-specific canopy heights aligns with additional site-level (Walker et al. 2006, Hudson et al. 2011, Myers-Smith et al. 2011a) and biome-level (Bjorkman et al. accepted) evidence that suggest tundra communities are becoming taller.

Radial growth was not very sensitive to climate at this site (Myers-Smith et al. 2011c, 2015a), but primary and secondary growth in woody species are not necessarily controlled by the same factors as shrubs can allocate resources to axial growth, new stems or below-ground biomass (Bret-Harte et al. 2002). Shrub growth at this site appears to be much more clonal than at other tundra locations with highly interconnected root matrices below ground. Under these growing conditions, plant-plant competition or access to nutrients and other resources may be more important controls over interannual variation in growth than variation in growing season climate (S Angers-Blondin and IH Myers-Smith, unpublished data). Therefore, the lack of a positive trend in radial growth (Figure 7c) is not incompatible with the simultaneous observed expansion and vertical growth of willows on Qikiqtaruk.

Total vegetation cover increased in all monitoring plots (Figure 8), concurrent with observations of increased plant biomass across tundra communities (Hudson and Henry 2009, Elmendorf et al. 2012b, Hobbie et al. 2017). All functional groups showed absolute increases in abundance except for lichens, which declined over the monitoring period as observed at a number of other sites (Joly et al. 2009,

Hobbie et al. 2017). Increases in vegetation cover corresponded with a reduction in bare ground, which could result from a deeper active layer depth (Figure 4, (Burn and Zhang 2009) and decreased cryoturbation that can influence surface vegetation (Walker et al. 2004). Within communities, graminoids and deciduous shrubs showed the greatest increase in abundance, aligning with community composition changes both on Qikiqtaruk (Kennedy et al. 2001, Myers-Smith et al. 2011b) and across the tundra biome (Elmendorf et al. 2012b, Hobbie et al. 2017). However, functional group responses were largely driven by species specific changes, notably for example the increase in graminoids as a result of increases in the species *Eriophorum vaginatum*, *Arctagrostis latifolia* and *Alopecurus alpinus*, and did not necessarily represent the response of all species within each functional group. Finally, rapid colonization of several plots by two graminoid species, *Arctagrostis latifolia* (Kennedy et al. 2001) and *Alopecurus alpinus*, indicates that community change can occur quickly over a period of a few years, despite low recruitment rates and slow growth associated with most tundra plants (Elmendorf et al. 2012b, 2015).

Attribution of vegetation change observations to environmental change

Environmental change observed at this site include spring, summer, autumn and winter warming, fewer frost days, earlier snow melt, decreased sea ice extent, warming soil temperatures and increases in active layer depth across the period of ecological monitoring (Figure 3). We also observed advancing spring plant phenology (Figure 6). According to our multi-parameter analysis (Figure 10), one of the most likely mechanisms driving the observed vegetation changes is increased growing season length and the resulting environmental changes including greater active layer depths and permafrost thaw. Although growing season length and resulting ecosystem-level impacts have been acknowledged as a potential driver of tundra vegetation change (Barichivich et al. 2013), few studies have tested the influence of growing season length relative to other environmental variables such as summer

temperature in tundra ecosystems (Khorsand Rosa et al. 2015). The differences in species-level responses may also have implications for vegetation change at the plant community level, if more responsive species are better able to take advantage of changing conditions (Cleland et al. 2012). For example, we found that *Dryas integrifolia* exhibited both the least phenological change and smallest relative increase in percent cover of the three monitored species over the 18-year ecological monitoring period. However, the extent to which plant phenology change will influence community-level responses to warming as a whole remains unclear (Wolkovich et al. 2012, Ernakovich et al. 2014, Prevéy et al. 2017).

Influence of changing active layer depth on the observed vegetation change

We hypothesize that some part of the vegetation change observed on Qikiqtaruk is an indirect effect of increased autumn temperatures on active layer depth. Qikiqtaruk is underlain by ice-rich permafrost that has warmed in recent decades (Burn and Zhang 2009, Figures 3h and 4a). The active layer at a site near the long-term vegetation monitoring plots has deepened by about 15-25 cm since 1985, reaching depths of ca. 45-55 cm (Burn and Zhang 2009) and as much as 87 cm depth by 2017 (Figure 4). Higher autumn temperatures are likely to delay refreezing of the active layer, leading to a nutrient release that could be used by plants in the following growing season (Blume-Werry et al. 2016, Salmon et al. 2016, Keuper et al. 2017). A deeper active layer also increases rooting depth and decreases surface disturbance from cryoturbation (Walker et al. 2004, Iversen et al. 2015, Wang et al. 2017, Keuper et al. 2017). In our study, we documented deeper active layers than previously reported, with warmer minimum soil temperatures at 12, 15 and 16 m soil depths (Figures 3h and 4, Table S2). Our results suggest permafrost thaw and a trend of a deeper active layer over time at this site, as has been observed at other locations (Burn and Zhang 2009, Liljedahl et al. 2016, Hobbie et al. 2017) concurrent with evidence of increasing thermokarst disturbances in the western Arctic (Lantz and Kokelj 2008,

Jorgenson et al. 2015, Segal et al. 2016, Kokelj et al. 2017), which could be changing available nutrients, rooting depths, surface cryoturbation and hydrology influencing plant cover and composition.

Influence of herbivory on the observed vegetation change

Observed tundra vegetation change at this site could in part be driven by variable herbivory due to cyclic lemming populations or spatial variation in muskox and caribou herbivory and/or trampling (Wal 2006, Olofsson et al. 2009, Kerby and Post 2013, Barrio et al. 2016). Key herbivores on Qikiqtaruk include muskox (*Ovibos moschatus*), caribou (*Rangifer tarandus caribou*), collared lemming (*Dicrostonyx groenlandicus*), brown lemming (*Lemmus trimucronatus*), tundra vole (*Microtus oeconomus*), and insects (Myers-Smith et al. 2011b). Ranger observations indicate that large mammals (muskox and caribou) on Qikiqtaruk are either increasing or fluctuating in unpredictable ways over the monitoring period from 1999 to 2017 (Cooley *et al.*, 2012, C Eckert, unpublished data). However, large herbivore group sizes and numbers of groups may not reflect herbivory pressure at the specific locations of the ecological monitoring plots. Lemmings follow 3–5 year cycles and vole populations and have relatively constant populations over longer time periods (Krebs et al. 2011). We began monitoring herbivory sign in 2014, but there are currently too few years of data to assess trends in herbivore impacts over time. An observed increase of herbivores could limit shrub or other vegetation increases (Olofsson et al. 2009), counter to the trends observed in this study. Exclusion of large herbivores over a two-year period on Qikiqtaruk also did not influence plant biomass (S Gilbert, D Reid, CJ Krebs and IH Myers-Smith, unpublished data); however, substantial herbivore impacts might only be observable over decades of exclusion (Olofsson 2006). Overall, the available evidence currently indicates that recent vegetation change on Qikiqtaruk is not primarily driven by changes in herbivory.

Other factors influencing the observed vegetation change at this site

Changes detected by ecological monitoring programs such as those observed in this study can be driven by a combination of site-level, regional or large-scale anthropogenic changes. Other factors that could be influencing tundra plant growth at this site include increasing atmospheric nitrogen deposition (Mack et al. 2004, Bobbink et al. 2010, Formica et al. 2014), increasing atmospheric CO_2 concentration (Wigley et al. 2010, Buitenwerf et al. 2012, Bond and Midgley 2012) and land-use change (Forbes et al. 2001, Kumpula et al. 2011) including recovery from the impacts of European whalers over wintering on the island for successive seasons from over 100 years ago (Burn 2012). However, statistically attributing vegetation changes to different ecological variables with varying extents of influence that have low inter-annual variability and correlate with each other is a major challenge in global change research.

Impacts of the vegetation change observed at this site

The observed vegetation changes on Qikiqtaruk could have substantial impacts on wildlife. Increased plant cover and growth could alter forage availability for large herbivores such as caribou (Joly et al. 2009, 2010), and could provide shelter for predator avoidance in small mammals (Wheeler and Hik 2014) or nesting habitat for birds (Boelman et al. 2015) for birds. For example, increased cover and abundance of tall shrub species, particularly in riparian areas, are likely altering bird habitats and changes in spring phenology can alter the timing of nesting of bird species on the island (Grabowski et al. 2013). Bird species that prefer shrub habitat of greater than 50 cm in height, specifically White-crowned Sparrow (*Zonotrichia leucophrys*), appear to be showing an increasing trend on Qikiqtaruk (C Eckert, unpublished data), and other shrub-nesting species may well increase there in the future (Cooley et al. 2012). Anecdotal observations indicate declines at Qikiqtaruk in two tundra nesting shorebirds, American Golden-Plover (*Pluvialis dominica*) and Ruddy Turnstone (*Arenaria interpres*, C

Eckert, unpublished data), species that nest on sparsely vegetated habitats associated with dry tundra and bare ground habitats. However, these species are also exhibiting continent-wide declines (Munro 2017), thus declines on Qikiqtaruk could be a function of both subtle changes to local breeding habitat (Wauchope et al. 2017), and population declines of these migratory birds across their ranges (Bart et al. 2007). Increased canopy heights could also change winter snow depths due to snow trapping (Myers-Smith and Hik 2013) and thus influence the ease of travel for large mammals. Finally, changes in temperature and plant phenology can alter fruit and berry production (Krebs et al. 2009), or create phenological mismatch among plant and animal species including birds and insect pollinators (McKinnon et al. 2012, Høye et al. 2013, Wheeler et al. 2014). All of these changes have the potential to restructure Arctic food webs and the interactions among plant and animal species, thus potentially altering wildlife species upon which humans depend (Stern and Gaden 2015).

Implications for the observed biome-wide tundra greening

The results presented in our study demonstrate substantial ecological changes across a broad range of ecological parameters at this focal study site. One challenge is understanding how representative these ecological changes are of vegetation change across the western Arctic region and tundra biome as a whole. To address this challenge, coarse-grain, remotely-sensed data are often employed to scale local observations to larger regions (Forbes et al. 2010, Macias-Fauria et al. 2012, Raynolds et al. 2013, Pattison et al. 2015, Walker et al. 2016). While there are often strong relationships between remotely sensed and *in situ* observations of ecological change (Forbes et al. 2010, Macias-Fauria et al. 2012, Raynolds et al. 2013, Pattison et al. 2015, Ju and Masek 2016), different time series of satellite data can show low correspondence (Guay et al. 2014) and analysis of remotely-sensed data suggests that the greening of the North American Arctic region has slowed in recent years (Bhatt et al. 2013, 2017). Our results indicate ongoing increase in canopy height and abundance of plants in the ecological monitoring

plots reported in our study (Figures 7 and 8); which is inconsistent with the saturation of greening patterns in satellite observations. The discrepancy between remotely sensed and *in situ* observations may be due to a mismatch in scales of observation, and hence there is a need to bridge the scale gap between high quality on-the-ground monitoring and remotely sensed observations of ecological changes.

Impacts of long-term ecological monitoring observations on ecosystems

While long-term monitoring provides unique and valuable insight into a system, there are inevitably caveats associated with regular visits to a site. Over time, we have noticed increased disturbance around the phenology transects due to trampling. We found that metal tags on plants tend to damage leaves and stems over time, and have moved to using adjacent marker stakes rather than marking the plants themselves. New technologies make it easier to monitor some aspects of ecological change with minimal physical impacts on the vegetation, and we are working to integrate automated data collection (e.g., time-lapse photography using phenocams) and remotely-acquired information (e.g., drone-based data collection) with our monitoring program. In recent years, the ecological monitoring program has expanded to include proximal remote sensing of the landscape, using drones (a.k.a. remotely piloted aircraft systems or unmanned aerial vehicles) to acquire image data (Figure 2b &c). These drone-acquired data can provide accurate and fine-grain measurements of both the spectral and structural properties of vegetation (e.g., Fraser et al. 2016). We are now incorporating phenocams to monitor vegetation change and timing of phenological events (Westergaard-Nielsen et al. 2017), and motion-triggered camera traps to quantify wildlife habitat use on the island (Tape and Gustine 2014) into the ecological monitoring program (Figure 2). Analysis of novel data, in conjunction with the multi-parameter monitoring program, will help us to understand what satellite observations of the landscape can and cannot reveal about ecological changes at this focal research site and more widely across the

Arctic. Nevertheless, collecting long-term, ground-based data is as important as ever, and we call for thoughtful planning of future monitoring programs to lessen direct anthropogenic pressures on field sites.

Conclusions

The 18 years of ecological monitoring on Qikiqtaruk indicate: 1) an increase in the potential growing season length with warmer air and soil temperatures, fewer frost days and earlier snow melt, leaf emergence and flowering of monitored plant species, yet also earlier leaf senescence, 2) an increase in canopy heights of tundra plant species, and 3) changing vegetation community composition, including increases in shrub and graminoid species and decreases in bare ground corresponding with a deepening active layer. Multi-parameter ecological monitoring has allowed for a much-improved understanding of ecological change at this site, suggesting that growing season length and active layer depths, rather than summer temperatures alone or changing herbivory, are likely the most important drivers of the observed vegetation change. Overall our findings align closely with reported individual trends for the western Arctic region (Stern and Gaden 2015) and across the tundra biome as a whole (Myers-Smith et al. 2011a, Elmendorf et al. 2012b, 2015, Oberbauer et al. 2013). However, this study is one of the first to demonstrate such a range of changes occurring simultaneously at one site over a period of decades, providing very strong evidence for ongoing, directional vegetation change and offering insight into the potential drivers of change. Our study highlights the critical role that collaborations between local people, park rangers, government scientists and academic research programs play in global change research. It is only with the multiple lines of evidence collected through an integrated ecological monitoring program that we can synthesize observed vegetation changes and compare potential drivers, thus improving our understanding of global change responses of this tundra ecosystem.

Acknowledgements

We thank the Herschel Island-Qikiqtaruk Territorial Park management, Catherine Kennedy, Dorothy Cooley, and Dr. Jill F. Johnstone for establishing and maintaining the phenology and composition data from Qikiqtaruk. We thank previous rangers including LeeJohn Meyook, Jordan McLeod, Pierre Foisy, Colin Gordon, Jeremy Hansen, Albert Rufus and field assistants including Santeri Lehtonen, William Palmer, Louise Beveridge, Clara Flintrop, John Godlee, Eleanor Walker, Catherine Henry and Anika Trimble. We thank Sigrid S. Nielsen and Prof. Christopher Burn for providing feedback on the manuscript. We thank the Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research for providing logistical support for this research and in particular Prof. Hugues Lantuit. Funding was provided by Herschel Island-Qikiqtaruk Territorial Park and the UK Natural Environment Research Council ShrubTundra Grant (NE/M016323/1), and we thank the NERC GEF for loan of GNSS equipment (NERC GEF:1063 and GEF:1064). Haydn Thomas and Jakob Assmann were funded by a NERC doctoral training partnership grant (NE/L002558/1). Sandra Angers-Blondin was funded by NSERC and the Canadian Centennial Scholarship Fund. Meagan Grabowski was funded by NSERC and Yukon Parks. Data are available through the Polar Data Catalogue (DOI to be added at time of publication). We thank the Inuvialuit People for the opportunity to conduct research on their traditional lands.

References

Ackerman, D., D. Griffin, S. E. Hobbie, and J. C. Finlay. 2017. Arctic shrub growth trajectories differ across soil moisture levels. Global Change Biology:n/a-n/a.

Andrews, C., J. Dick, C. Jonasson, and T. Callaghan. 2011. Assessment of Biological and Environmental Phenology at a Landscape Level from 30 Years of Fixed-Date Repeat Photography in Northern Sweden. AMBIO: A Journal of the Human Environment 40:600–609.

Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G. H. R. Henry, M. H. Jones, R. D. Hollister, I. S. Jónsdóttir, K. Laine, E. Lévesque, G. M. Marion, U. Molau, P. Mølgaard, U. Nordenhäll, V. Raszhivin, C. H. Robinson, G. Starr, A. Stenström, M. Stenström, Ø. Totland, P. L. Turner, L. J. Walker, P. J. Webber, J. M. Welker, and P. A. Wookey. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. Ecological Monographs 69:491–511.

Barichivich, J., K. R. Briffa, R. B. Myneni, T. J. Osborn, T. M. Melvin, P. Ciais, S. Piao, and C. Tucker. 2013. Large-scale variations in the vegetation growing season and annual cycle of atmospheric CO2 at high northern latitudes from 1950 to 2011. Global Change Biology 19:3167–3183.

Barrio, I. C., D. S. Hik, I. S. Jónsdóttir, C. G. Bueno, M. A. Mörsdorf, and V. T. Ravolainen. 2016. Herbivory Network: An international, collaborative effort to study herbivory in Arctic and alpine ecosystems. Polar Science 10:297–302.

Bart, J., S. Brown, B. Harrington, and R. I. Guy Morrison. 2007. Survey trends of North American shorebirds: population declines or shifting distributions? Journal of Avian Biology 38:73–82.

Beck, P. S. A., and S. J. Goetz. 2011. Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. Environmental Research Letters 6:045501.

628 Bhatt, U. S., D. A. Walker, M. K. Raynolds, P. A. Bieniek, H. E. Epstein, J. C. Comiso, J. E. Pinzon, C.
629 J. Tucker, and I. V. Polyakov. 2013. Recent Declines in Warming and Vegetation Greening
630 Trends over Pan-Arctic Tundra. Remote Sensing 5:4229–4254.
631 Bhatt, U. S., D. A. Walker, M. K. Raynolds, P. A. Bieniek, H. E. Epstein, J. C. Comiso, J. E. Pinzon, C.
632 J. Tucker, M. Steele, W. Ermold, and J. Zhang. 2017. Changing seasonality of panarctic tundra
633 vegetation in relationship to climatic variables. Environmental Research Letters 12:055003.
634 Bhatt, U. S., D. A. Walker, M. K. Raynolds, J. C. Comiso, H. E. Epstein, G. J. Jia, R. Gens, J. E.
635 Pinzon, C. J. Tucker, C. E. Tweedie, and P. J. Webber. 2010. Circumpolar arctic tundra
636 vegetation change is linked to sea ice decline. Earth Interactions 14:1–20.
637 Bjorkman, A. D., S. C. Elmendorf, A. L. Beamish, M. Vellend, and G. H. R. Henry. 2015a. Contrasting
638 effects of warming and increased snowfall on Arctic tundra plant phenology over the past two
639 decades. Global Change Biology 21:4651–4661.
640 Bjorkman, A. D., S. C. Elmendorf, A. L. Beamish, M. Vellend, and G. H. R. Henry. 2015b. Contrasting
641 effects of warming and increased snowfall on Arctic tundra plant phenology over the past two
642 decades. Global Change Biology 21:4651–4661.
643 Bjorkman, A. D., I. H. Myers-Smith, H. J. D. Thomas, S. C. Elmendorf, sTundra, ITEX, and Tundra
644 Trait Team. (n.d.). Changes in plant functional traits across a warming tundra biome. Accepted
645 at Nature (ref: 2017-09-12391).
646 Blume-Werry, G., S. D. Wilson, J. Kreyling, and A. Milbau. 2016. The hidden season: growing season
647 is 50% longer below than above ground along an arctic elevation gradient. New Phytologist
648 209:978–986.
649 Bobbink, R., K. Hicks, J. Galloway, T. Spranger, R. Alkemade, M. Ashmore, M. Bustamante, S.
650 Cinderby, E. Davidson, F. Dentener, B. Emmett, J.-W. Erisman, M. Fenn, F. Gilliam, A.

Nordin, L. Pardo, and W. De Vries. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications 20:30–59.

Boelman, N. T., L. Gough, J. Wingfield, S. Goetz, A. Asmus, H. E. Chmura, J. S. Krause, J. H. Perez, S. K. Sweet, and K. C. Guay. 2015. Greater shrub dominance alters breeding habitat and food resources for migratory songbirds in Alaskan arctic tundra. Global Change Biology 21:1508–1520.

Bond, W. J., and G. F. Midgley. 2012. Carbon dioxide and the uneasy interactions of trees and savannah grasses. Phil. Trans. R. Soc. B 367:601–612.

Bret-Harte, M. S., E. A. García, V. M. Sacré, J. R. Whorley, J. L. Wagner, S. C. Lippert, and F. S. Chapin. 2004. Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. Journal of Ecology 92:635–647.

Bret-Harte, M. S., G. R. Shaver, and F. S. Chapin. 2002. Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change. Journal of Ecology 90:251–267.

Buitenwerf, R., W. J. Bond, N. Stevens, and W. S. W. Trollope. 2012. Increased tree densities in South African savannas: >50 years of data suggests CO2 as a driver. Global Change Biology 18:675–684.

Burn, C. R. 2012. Herschel Island Qikiqtaryuk: A Natural and Cultural History of Yukon's Arctic Island. Calgary University Press, Calgary, Alberta, Canada.

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

CAFF. 2013. Arctic Biodiversity Assessment: Status and Trends in Arctic Biodiversity. Akureyri.

673 Callaghan, T. V., F. Bergholm, T. R. Christensen, C. Jonasson, U. Kokfelt, and M. Johansson. 2010. A
674 new climate era in the sub-Arctic: Accelerating climate changes and multiple impacts.
675 Geophysical Research Letters 37:L14705.
676 Callaghan, T. V., C. Jonasson, T. Thierfelder, Z. Yang, H. Hedenås, M. Johansson, U. Molau, R. V.
677 Bogaert, A. Michelsen, J. Olofsson, D. Gwynn-Jones, S. Bokhorst, G. Phoenix, J. W. Bjerke, H.
678 Tømmervik, T. R. Christensen, E. Hanna, E. K. Koller, and V. L. Sloan. 2013. Ecosystem
679 change and stability over multiple decades in the Swedish subarctic: complex processes and
680 multiple drivers. Phil. Trans. R. Soc. B 368:20120488.
681 Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E.
682 M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate
683 change. Ecology 93:1765–1771.
684 Cooley, D., C. D. Eckert, and R. R. Gordon. 2012. Herschel Island—Qikiqtaruk Inventory, Monitoring,
685 and Research Program. Page 45. Yukon Parks, Whitehorse, YT.
686 Dormann, C. F., R. Van Der Wal, and S. J. Woodin. 2004. Neighbour identity modifies effects of
687 elevated temperature on plant performance in the High Arctic. Global Change Biology
688 10:1587–1598.
689 Ellebjerg, S. M., M. P. Tamstorf, L. Illeris, A. Michelsen, and B. U. Hansen. 2008. Inter-annual
690 variability and controls of plant phenology and productivity at Zackenberg. Advances in
691 Ecological Research 40:249–273.
692 Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, A. D. Bjorkman, T. V. Callaghan, L. S.
693 Collier, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, A. M. Fosaa, W. A. Gould, J.
694 Grétarsdóttir, J. Harte, L. Hermanutz, D. S. Hik, A. Hofgaard, F. Jarrad, I. S. Jónsdóttir, F.
695 Keuper, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, S. I. Lang, V. Loewen, J. L. May, J.
696 Mercado, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, S. Pieper, E. Post, C.

Rixen, C. H. Robinson, N. M. Schmidt, G. R. Shaver, A. Stenström, A. Tolvanen, Ø. Totland, T. Troxler, C. Wahren, P. J. Webber, J. M. Welker, and P. A. Wookey. 2012a. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. Ecology Letters 15:164–175.

Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, N. Boulanger-Lapointe, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, E. Dorrepaal, T. G. Elumeeva, M. Gill, W. A. Gould, J. Harte, D. S. Hik, A. Hofgaard, D. R. Johnson, J. F. Johnstone, I. S. Jónsdóttir, J. C. Jorgenson, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, M. Lara, E. Lévesque, B. Magnússon, J. L. May, J. A. Mercado-Dı´az, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, V. G. Onipchenko, C. Rixen, N. M. Schmidt, G. R. Shaver, M. J. Spasojevic, Þ. E. Þórhallsdóttir, A. Tolvanen, T. Troxler, C. E. Tweedie, S. Villareal, C.-H. Wahren, X. Walker, P. J. Webber, J. M. Welker, and S. Wipf. 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change 2:453–457.

Elmendorf, S., G. H. R. Henry, R. D. Hollister, A. M. Fosaa, W. a. Gould, L. Hermanutz, A. Hofgaard, I. I. Jónsdóttir, J. C. Jorgenson, E. Lévesque, B. Magnusson, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, C. Rixen, C. E. Tweedie, and M. Walker. 2015. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. Proceedings of the National Academy of Sciences 112:448–452.

Ernakovich, J. G., K. A. Hopping, A. B. Berdanier, R. T. Simpson, E. J. Kachergis, H. Steltzer, and M. D. Wallenstein. 2014. Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. Global Change Biology.

Forbes, B. C., J. J. Ebersole, and B. Strandberg. 2001. Anthropogenic disturbance and patch dynamics in circumpolar arctic ecosystems. Conservation Biology 15:954–969.

720 Forbes, B. C., M. Macias-Fauria, and P. Zetterberg. 2010. Russian arctic warming and “greening” are
721 closely tracked by tundra shrub willows. Global Change Biology 16:1542–1554.
722 Forkel, M., N. Carvalhais, C. Rödenbeck, R. Keeling, M. Heimann, K. Thonicke, S. Zaehle, and M.
723 Reichstein. 2016. Enhanced seasonal CO2 exchange caused by amplified plant productivity in
724 northern ecosystems. Science 351:696–699.
725 Formica, A., E. C. Farrer, I. W. Ashton, and K. N. Suding. 2014. Shrub expansion over the past 62
726 years in rocky mountain alpine tundra: Possible causes and consequences. Arctic, Antarctic, and
727 Alpine Research 46:616–631.
728 Fraser, R. H., I. Olthof, M. Carrière, a Deschamps, and D. Pouliot. 2011. Detecting long-term changes
729 to vegetation in northern Canada using the Landsat satellite image archive. Environmental
730 Research Letters 6:045502.
731 Fraser, R. H., I. Olthof, T. C. Lantz, and C. Schmitt. 2016. UAV photogrammetry for mapping
732 vegetation in the low-Arctic. Arctic Science 2:79–102.
733 Gamon, J. a., K. F. Huemmrich, R. S. Stone, and C. E. Tweedie. 2013. Spatial and temporal variation
734 in primary productivity (NDVI) of coastal Alaskan tundra: Decreased vegetation growth
735 following earlier snowmelt. Remote Sensing of Environment 129:144–153.
736 Gelman, A., and D. B. Rubin. 1992. Inference from Iterative Simulation Using Multiple Sequences.
737 Statistical Science 7:457–472.
738 Gill, H., and T. Lantz. 2014. A Community-Based Approach to Mapping Gwich’in Observations of
739 Environmental Changes in the Lower Peel River Watershed, NT. Journal of Ethnobiology
740 34:294–314.
741 Grabowski, M. M., F. I. Doyle, D. G. Reid, D. Mossop, and D. Talarico. 2013. Do Arctic-nesting birds
742 respond to earlier snowmelt? A multi-species study in north Yukon, Canada. Polar Biology
743 36:1097–1105.

744 Guay, K. C., P. S. A. Beck, L. T. Berner, S. J. Goetz, A. Baccini, and W. Buermann. 2014. Vegetation
745 productivity patterns at high northern latitudes: a multi-sensor satellite data assessment. Global
746 Change Biology 20:3147–3158.
747 Hadfield, J. D. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The
748 MCMCglmm R Package 33:1–22.
749 Harris, Ian. 2013. CRU TS3.21: Climatic Research Unit (CRU) Time-Series (TS) Version 3.21 of High
750 Resolution Gridded Data of Month-by-month Variation in Climate (Jan. 1901 - Dec. 2012).
751 NERC British Atmospheric Data Centre.
752 Hobbie, J. E., G. R. Shaver, E. B. Rastetter, J. E. Cherry, S. J. Goetz, K. C. Guay, W. A. Gould, and G.
753 W. Kling. 2017. Ecosystem responses to climate change at a Low Arctic and a High Arctic
754 long-term research site. Ambio 46:160–173.
755 Høye, T. T., E. Post, H. Meltofte, N. M. Schmidt, and M. C. Forchhammer. 2007. Rapid advancement
756 of spring in the High Arctic. Current Biology 17:R449–R451.
757 Høye, T. T., E. Post, N. M. Schmidt, K. Trøjelsgaard, and M. C. Forchhammer. 2013. Shorter
758 flowering seasons and declining abundance of flower visitors in a warmer Arctic. Nature
759 Climate Change 3:759–763.
760 Hudson, J., and G. Henry. 2009. Increased plant biomass in a High Arctic heath community from 1981
761 to 2008. Ecology 90:2657–2663.
762 Hudson, J. M. G., and G. H. R. Henry. 2010. High Arctic plant community resists 15 years of
763 experimental warming. Journal of Ecology 98:1035–1041.
764 Hudson, J. M. G., G. H. R. Henry, and W. K. Cornwell. 2011. Taller and larger: shifts in Arctic tundra
765 leaf traits after 16 years of experimental warming. Global Change Biology 17:1013–1021.

766 Iler, A. M., T. T. Høye, D. W. Inouye, and N. M. Schmidt. 2013. Nonlinear flowering responses to
767 climate: are species approaching their limits of phenological change? Philosophical
768 Transactions of the Royal Society of London B: Biological Sciences 368:20120489.
769 IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to
770 the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.
771 IPCC. 2014. Climate change 2014: impacts, adaptation, and vulnerability. Contribution of Working
772 Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate
773 Change:1042.
774 Iversen, C. M., V. L. Sloan, P. F. Sullivan, E. S. Euskirchen, A. D. McGuire, R. J. Norby, A. P.
775 Walker, J. M. Warren, and S. D. Wullschleger. 2015. The unseen iceberg: plant roots in arctic
776 tundra. New Phytologist 205:34–58.
777 Jia, G. J., H. E. Epstein, and D. A. Walker. 2009. Vegetation greening in the Canadian Arctic related to
778 decadal warming. Journal of Environmental Monitoring 11:2231.
779 Joly, K., M. J. Cole, and R. R. Jandt. 2010. Diets of overwintering caribou, Rangifer tarandus, track
780 decadal changes in Arctic tundra vegetation. The Canadian Field-Naturalist 121:379–383.
781 Joly, K., R. R. Jandt, and D. R. Klein. 2009. Decrease of lichens in Arctic ecosystems: the role of
782 wildfire, caribou, reindeer, competition and climate in north-western Alaska. Polar Research
783 28:433–442.
784 Jorgenson, J. C., M. K. Raynolds, J. H. Reynolds, and A.-M. Benson. 2015. Twenty-five year record of
785 changes in plant cover on tundra of northeastern Alaska. Arctic, Antarctic, and Alpine Research
786 47:785–806.
787 Ju, J., and J. G. Masek. 2016. The vegetation greenness trend in Canada and US Alaska from 1984–
788 2012 Landsat data. Remote Sensing of Environment 176:1–16.

789 Keenan, T. F., and A. D. Richardson. 2015. The timing of autumn senescence is affected by the timing
790 of spring phenology: implications for predictive models. Global Change Biology 21:2634–
791 2641.
792 Kennedy, C. E., C. A. S. Smith, and D. A. Cooley. 2001. Observations of Change in the Cover of
793 Polargrass, Arctagrostis latifolia, and Arctic Lupine, Lupinus arcticus, in Upland Tundra on
794 Herschel Island, Yukon Territory. Canadian Field-Naturalist 115:323–328.
795 Kerby, J. T., and E. Post. 2013. Advancing plant phenology and reduced herbivore production in a
796 terrestrial system associated with sea ice decline. Nature communications 4:2514.
797 Keuper, F., E. Dorrepaal, P. M. van Bodegom, R. van Logtestijn, G. Venhuizen, J. van Hal, and R.
798 Aerts. 2017. Experimentally increased nutrient availability at the permafrost thaw front
799 selectively enhances biomass production of deep-rooting subarctic peatland species. Global
800 Change Biology 23:4257–4266.
801 Khorsand Rosa, R., S. F. Oberbauer, G. Starr, I. Parker La Puma, E. Pop, L. Ahlquist, and T. Baldwin.
802 2015. Plant phenological responses to a long-term experimental extension of growing season
803 and soil warming in the tussock tundra of Alaska. Global Change Biology 21:4520–4532.
804 Klady, R. A., G. H. R. Henry, and V. Lemay. 2011. Changes in high arctic tundra plant reproduction in
805 response to long-term experimental warming. Global Change Biology 17:1611–1624.
806 Kokelj, S. V., T. C. Lantz, J. Tunnicliffe, R. Segal, and D. Lacelle. 2017. Climate-driven thaw of
807 permafrost preserved glacial landscapes, northwestern Canada. Geology 45:371–374.
808 Körner, C., and D. Basler. 2010. Phenology Under Global Warming. Science 327:1461–1462.
809 Krebs, C. J., R. Boonstra, K. Cowcill, and A. J. Kenney. 2009. Climatic determinants of berry crops in
810 the boreal forest of the southwestern Yukon. Botany 87:401–408.
811 Krebs, C. J., D. Reid, A. J. Kenney, and S. Gilbert. 2011. Fluctuations in lemming populations in north
812 Yukon, Canada, 2007–2010. Canadian Journal of Zoology 89:297–306.

Kumpula, T., A. Pajunen, E. Kaarlejärvi, B. C. Forbes, and F. Stammler. 2011. Land use and land cover change in arctic Russia: Ecological and social implications of industrial development. Global Environmental Change 21:550–562.

Lang, S. I., J. H. C. Cornelissen, G. R. Shaver, M. Ahrens, T. V. Callaghan, U. Molau, C. J. F. Ter Braak, A. Hölzer, and R. Aerts. 2012. Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. Global Change Biology 18:1096–1107.

Lantz, T. C., S. E. Gergel, and G. H. R. Henry. 2010. Response of green alder (Alnus viridis subsp. fruticosa) patch dynamics and plant community composition to fire and regional temperature in north-western Canada. Journal of Biogeography 37:1597–1610.

Lantz, T. C., and S. V. Kokelj. 2008. Increasing rates of retrogressive thaw slump activity in the Mackenzie Delta region, N.W.T., Canada. Geophysical Research Letters 35:5 PP.

Lantz, T. C., S. V. Kokelj, S. E. Gergel, and G. H. R. Henry. 2009. Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps. Global Change Biology 15:1664–1675.

Lantz, T. C., P. Marsh, and S. V. Kokelj. 2013. Recent shrub proliferation in the Mackenzie Delta Uplands and microclimatic implications. Ecosystems 16:47–59.

Legault, G., and M. Cusa. 2015. Temperature and delayed snowmelt jointly affect the vegetative and reproductive phenologies of four sub-Arctic plants. Polar Biology 38:1701–1711.

Liljedahl, A. K., J. Boike, R. P. Daanen, A. N. Fedorov, G. V. Frost, G. Grosse, L. D. Hinzman, Y. Iijma, J. C. Jorgenson, N. Matveyeva, M. Necsoiu, M. K. Raynolds, V. E. Romanovsky, J. Schulla, K. D. Tape, D. A. Walker, C. J. Wilson, H. Yabuki, and D. Zona. 2016. Pan-Arctic ice-wedge degradation in warming permafrost and its influence on tundra hydrology. Nature Geoscience 9:312–318.

837 Macias-Fauria, M., B. C. Forbes, P. Zetterberg, and T. Kumpula. 2012. Eurasian Arctic greening
838 reveals teleconnections and the potential for structurally novel ecosystems. Nature Climate
839 Change 2:613–618.
840 Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin. 2004. Ecosystem
841 carbon storage in Arctic tundra reduced by long-term nutrient fertilization. Nature 431:440–
842 443.
843 Martin, A. C., E. S. Jeffers, G. Petrokofsky, I. Myers-Smith, and M. Macias-Fauria. 2017. Shrub
844 growth and expansion in the Arctic tundra: an assessment of controlling factors using an
845 evidence-based approach. Environmental Research Letters 12:085007.
846 McKinnon, L., M. Picotin, E. Bolduc, C. Juillet, and J. Bêty. 2012. Timing of breeding, peak food
847 availability, and effects of mismatch on chick growth in birds nesting in the High Arctic.
848 Canadian Journal of Zoology 90:961–971.
849 Moffat, N. D., T. C. Lantz, R. H. Fraser, and I. Olthof. 2016. Recent Vegetation Change (1980–2013)
850 in the Tundra Ecosystems of the Tuktoyaktuk Coastlands, NWT, Canada. Arctic, Antarctic, and
851 Alpine Research 48:581–597.
852 Molau, U., and P. Mølgaard. 1996. International Tundra Experiment (ITEX).
853 http://www.geog.ubc.ca/itex/library/index.php.
854 Munro, M. 2017. What's killing the world's shorebirds? Nature News 541:16.
855 Myers-Smith, I. H., S. C. Elmendorf, P. S. A. Beck, M. Wilmking, M. Hallinger, D. Blok, K. D. Tape,
856 S. A. Rayback, M. Macias-Fauria, B. C. Forbes, J. D. M. Speed, N. Boulanger-Lapointe, C.
857 Rixen, E. Lévesque, N. M. Schmidt, C. Baittinger, A. J. Trant, L. Hermanutz, L. S. Collier, M.
858 A. Dawes, T. C. Lantz, S. Weijers, R. H. Jørgensen, A. Buchwal, A. Buras, A. T. Naito, V.
859 Ravolainen, G. Schaepman-Strub, J. A. Wheeler, S. Wipf, K. C. Guay, D. S. Hik, and M.

Vellend. 2015a. Climate sensitivity of shrub growth across the tundra biome. Nature Climate Change 5:887–891.

Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M. Macias-Fauria, U. Sass-Klaassen, E. Lévesque, S. Boudreau, P. Ropars, L. Hermanutz, A. Trant, L. S. Collier, S. Weijers, J. Rozema, S. a Rayback, N. M. Schmidt, G. Schaepman-Strub, S. Wipf, C. Rixen, C. B. Ménard, S. Venn, S. Goetz, L. Andreu-Hayles, S. Elmendorf, V. Ravolainen, J. Welker, P. Grogan, H. E. Epstein, and D. S. Hik. 2011a. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6:045509.

Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M. Macias-Fauria, U. Sass-Klaassen, E. Lévesque, S. Boudreau, P. Ropars, L. Hermanutz, A. J. Trant, L. S. Collier, S. Weijers, J. Rozema, S. A. Rayback, N. M. Schmidt, G. Schaepman-Strub, S. Wipf, C. Rixen, C. B. Ménard, S. Venn, S. Goetz, L. Andreu-Hayles, S. Elmendorf, V. Ravolainen, J. Welker, P. Grogan, H. E. Epstein, and D. S. Hik. 2011b. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6:045509.

Myers-Smith, I. H., M. Hallinger, D. Blok, U. Sass-Klaassen, S. A. Rayback, S. Weijers, A. J. Trant, K. D. Tape, A. T. Naito, S. Wipf, C. Rixen, M. A. Dawes, J. A. Wheeler, A. Buchwal, C. Baittinger, M. Macias-Fauria, B. C. Forbes, E. Lévesque, N. Boulanger-Lapointe, I. Beil, V. Ravolainen, and M. Wilmking. 2015b. Methods for measuring arctic and alpine shrub growth: A review. Earth-Science Reviews 140:1–13.

Myers-Smith, I. H., D. Hik, C. Kennedy, C. Dorothy, J. Johnstone, A. Kenney, and C. Krebs. 2011c. Expansion of canopy-forming willows over the twentieth century on Herschel Island, Yukon Territory, Canada. Ambio 40:610–623.

884 Myers-Smith, I. H., and D. S. Hik. 2013. Shrub canopies influence soil temperatures but not nutrient
885 dynamics: An experimental test of tundra snow–shrub interactions. Ecology and Evolution
886 3:3683–3700.
887 Isla H., M., and H. David S. 2017. Climate warming as a driver of tundra shrubline advance. Journal of
888 Ecology 106:547–560.
889 Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, and R. R. Nemani. 1997. Increased plant growth
890 in the northern high latitudes from 1981 to 1991. , Published online: 17 April 1997; |
891 doi:10.1038/386698a0 386:698–702.
892 Naito, A. T., and D. M. Cairns. 2011. Patterns and processes of global shrub expansion. Progress in
893 Physical Geography 35:423–442.
894 Oberbauer, S. F., S. C. Elmendorf, T. G. Troxler, R. D. Hollister, A. V. Rocha, M. S. Bret-Harte, M. A.
895 Dawes, A. M. Fosaa, G. H. R. Henry, T. T. Høye, F. C. Jarrad, I. S. Jónsdóttir, K. Klanderud, J.
896 A. Klein, U. Molau, C. Rixen, N. M. Schmidt, G. R. Shaver, R. T. Slider, Ø. Totland, C.-H.
897 Wahren, and J. M. Welker. 2013. Phenological response of tundra plants to background climate
898 variation tested using the International Tundra Experiment. Philosophical Transactions of the
899 Royal Society B: Biological Sciences 368.
900 Obu, J., H. Lantuit, I. Myers-Smith, B. Heim, J. Wolter, and M. Fritz. 2015. Effect of Terrain
901 Characteristics on Soil Organic Carbon and Total Nitrogen Stocks in Soils of Herschel Island,
902 Western Canadian Arctic. Permafrost and Periglacial Processes 28:92–107.
903 Olofsson, J. 2006. Short- and long-term effects of changes in reindeer grazing pressure on tundra heath
904 vegetation. Journal of Ecology 94:431–440.
905 Olofsson, J., L. Oksanen, T. Callaghan, P. E. Hulme, T. Oksanen, and O. Suominen. 2009. Herbivores
906 inhibit climate-driven shrub expansion on the tundra. Global Change Biology 15:2681–2693.

907 Park, T., S. Ganguly, H. Tømmervik, E. S. Euskirchen, K.-A. Høgda, S. R. Karlsen, V. Brovkin, R. R.
908 Nemani, and R. B. Myneni. 2016. Changes in growing season duration and productivity of
909 northern vegetation inferred from long-term remote sensing data. Environmental Research
910 Letters 11:084001.
911 Pattison, R. R., J. C. Jorgenson, M. K. Raynolds, and J. M. Welker. 2015. Trends in NDVI and Tundra
912 Community Composition in the Arctic of NE Alaska Between 1984 and 2009. Ecosystems
913 18:707–719.
914 Pau, S., E. M. Wolkovich, B. I. Cook, T. J. Davies, N. J. B. Kraft, K. Bolmgren, J. L. Betancourt, and
915 E. E. Cleland. 2011. Predicting phenology by integrating ecology, evolution and climate
916 science. Global Change Biology 17:3633–3643.
917 Peñuelas, J., and I. Filella. 2001. Responses to a Warming World. Science 294:793–795.
918 Peñuelas, J., T. Rutishauser, and I. Filella. 2009. Phenology Feedbacks on Climate Change. Science
919 324:887–888.
920 Plummer, M. 2014. JAGS: Just another Gibbs sampler.
921 Plummer, M., N. Best, K. Cowles, and K. Vines. 2006. CODA: convergence diagnosis and output
922 analysis for MCMC. R News 6:7–11.
923 Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D.
924 Fox, O. Gilg, D. S. Hik, T. T. Hoye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D.
925 McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. van der
926 Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup. 2009a. Ecological dynamics
927 across the Arctic associated with recent climate change. Science 325:1355–1358.
928 Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V Callaghan, T. R. Christensen, B. Elberling, A. D.
929 Fox, O. Gilg, D. S. Hik, T. T. Hoye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D.
930 McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. van der

931 Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup. 2009b. Ecological dynamics
932 across the Arctic associated with recent climate change. Science 325:1355–1358.
933 Post, E., J. Kerby, C. Pedersen, and H. Steltzer. 2016. Highly individualistic rates of plant phenological
934 advance associated with arctic sea ice dynamics. Biology Letters 12:20160332.
935 Prevéy, J., M. Vellend, N. Rüger, R. D. Hollister, A. D. Bjorkman, I. H. Myers-Smith, S. C. Elmendorf,
936 K. Clark, E. J. Cooper, B. Elberling, A. M. Fosaa, G. H. R. Henry, T. T. Høye, I. S. Jónsdóttir,
937 K. Klanderud, E. Lévesque, M. Mauritz, U. Molau, S. M. Natali, S. F. Oberbauer, Z. A.
938 Panchen, E. Post, S. B. Rumpf, N. M. Schmidt, E. A. G. Schuur, P. R. Semenchuk, T. Troxler,
939 J. M. Welker, and C. Rixen. 2017. Greater temperature sensitivity of plant phenology at colder
940 sites: implications for convergence across northern latitudes. Global Change Biology:n/a-n/a.
941 R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for
942 Statistical Computing, Vienna, Austria. 2013.
943 Raynolds, M. K., D. A. Walker, D. Verbylaf, and C. A. Mungeri. 2013. Patterns of Change vs/^ithin a
944 Tundra Landscape: 22-year Landsat NDVI Trends in an Area of the Northern Foothills of the
945 Brooks Range, Alaska. Arctic, Antarctic, and Alpine Research 45:249–260.
946 Ropars, P., and S. Boudreau. 2012. Shrub expansion at the forest–tundra ecotone: spatial heterogeneity
947 linked to local topography. Environmental Research Letters 7:015501.
948 Salmon, V. G., P. Soucy, M. Mauritz, G. Celis, S. M. Natali, M. C. Mack, and E. A. G. Schuur. 2016.
949 Nitrogen availability increases in a tundra ecosystem during five years of experimental
950 permafrost thaw. Global Change Biology 22:1927–1941.
951 Schmidt, N., C. Baittinger, and M. Forchhammer. 2006. Reconstructing century-long snow regimes
952 using estimates of high arctic Salix arctica radial growth. Arctic, Antarctic, and Alpine
953 Research 38:257–262.

954 Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image
955 analysis. Nature Methods 9:671–675.
956 Segal, R. A., T. C. Lantz, and S. V. Kokelj. 2016. Acceleration of thaw slump activity in glaciated
957 landscapes of the Western Canadian Arctic. Environmental Research Letters 11:034025.
958 Smith, C. A. S., C. E. Kennedy, A. E. Hargrave, and K. M. McKenna. 1989. Soil and vegetation of
959 Herschel Island. Research Branch, Agriculture Canada.
960 Stern, G. 2015. From Science to Policy in the Western and Central Canadian Arctic: An Integrated
961 Regional Impact Study (IRIS) of Climate Change and Modernization. ArcticNet.
962 Stern, G., and A. Gaden. 2015. From science to policy in the western and central Canadian Arctic: An
963 integrated regional impact study (IRIS) of climate change and modernization. Page ArcticNet.
964 Su, Y.-S., and M. Yajima. 2012. R2jags: A Package for Running jags from R. R package version 0.03-
965 08, URL http://CRAN. R-project. org/package= R2jags.
966 Svoboda, J., B. Freedman, J. Calvert, and J. L. Murray. 1994. Ecology of a Polar Oasis: Alexandra
967 Fiord, Ellesmere Island, Canada. Captus University Publications.
968 Tape, K. D., and D. D. Gustine. 2014. Capturing Migration Phenology of Terrestrial Wildlife Using
969 Camera Traps. BioScience 64:117–124.
970 Tape, K. D., M. Sturm, and C. H. Racine. 2006. The evidence for shrub expansion in Northern Alaska
971 and the Pan-Arctic. Global Change Biology 12:686–702.
972 Tape, K., M. Hallinger, J. Welker, and R. Ruess. 2012. Landscape heterogeneity of shrub expansion in
973 Arctic Alaska. Ecosystems 15:711–724.
974 Wal, R. van der. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence
975 from the tundra. Oikos 114:177–186.
976 Walker, D. A., F. J. A. Daniëls, I. Alsos, U. S. Bhatt, A. L. Breen, M. Buchhorn, H. Bültmann, L. A.
977 Druckenmiller, M. E. Edwards, D. Ehrich, H. E. Epstein, W. A. Gould, R. A. Ims, H. Meltofte,

M. K. Raynolds, J. Sibik, S. S. Talbot, and P. J. Webber. 2016. Circumpolar Arctic vegetation: a hierarchic review and roadmap toward an internationally consistent approach to survey, archive and classify tundra plot data. Environmental Research Letters 11:055005.

Walker, D. A., H. E. Epstein, W. A. Gould, A. M. Kelley, A. N. Kade, J. A. Knudson, W. B. Krantz, G. Michaelson, R. A. Peterson, C.-L. Ping, M. K. Raynolds, V. E. Romanovsky, and Y. Shur. 2004. Frost-boil ecosystems: complex interactions between landforms, soils, vegetation and climate. Permafrost and Periglacial Processes 15:171–188.

Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jónsdóttir, J. A. Klein, B. Magnússon, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, Ø. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America 103:1342–1346.

Wang, P., J. Limpens, L. Mommer, J. van Ruijven, A. L. Nauta, F. Berendse, G. Schaepman-Strub, D. Blok, T. C. Maximov, and M. M. P. D. Heijmans. 2017. Above- and below-ground responses of four tundra plant functional types to deep soil heating and surface soil fertilization. Journal of Ecology 105:947–957.

Wauchope, H. S., J. D. Shaw, Ø. Varpe, E. G. Lappo, D. Boertmann, R. B. Lanctot, and R. A. Fuller. 2017. Rapid climate-driven loss of breeding habitat for Arctic migratory birds. Global Change Biology 23:1085–1094.

Westergaard-Nielsen, A., M. Lund, S. H. Pedersen, N. M. Schmidt, S. Klosterman, J. Abermann, and B. U. Hansen. 2017. Transitions in high-Arctic vegetation growth patterns and ecosystem productivity tracked with automated cameras from 2000 to 2013. Ambio 46:39–52.

Wheeler, H. C., and D. S. Hik. 2014. Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. Animal Behaviour 95:1–8.

Wheeler, H. C., T. T. Høye, N. M. Schmidt, J.-C. Svenning, and M. C. Forchhammer. 2014. Phenological mismatch with abiotic conditions - implications for flowering in Arctic plants. Ecology.

Wigley, B. J., W. J. Bond, and M. T. Hoffman. 2010. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? Global Change Biology 16:964–976.

Van Wijk, M. T., K. E. Clemmensen, G. R. Shaver, M. Williams, T. V. Callaghan, F. S. Chapin, J. H. C. Cornelissen, L. Gough, S. E. Hobbie, S. Jonasson, J. A. Lee, A. Michelsen, M. C. Press, S. J. Richardson, and H. Rueth. 2004. Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: Generalizations and differences in ecosystem and plant type responses to global change. Global Change Biology 10:105–123.

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

Wolkovich, E. M., J. Regetz, and M. I. O'Connor. 2012. Advances in global change research require open science by individual researchers. Global Change Biology 18:2102–2110.

Xu, L., R. B. Myneni, F. S. Chapin Iii, T. V. Callaghan, J. E. Pinzon, C. J. Tucker, Z. Zhu, J. Bi, P. Ciais, H. Tømmervik, E. S. Euskirchen, B. C. Forbes, S. L. Piao, B. T. Anderson, S. Ganguly, R. R. Nemani, S. J. Goetz, P. S. A. Beck, A. G. Bunn, C. Cao, and J. C. Stroeve. 2013. Temperature and vegetation seasonality diminishment over northern lands. Nature Climate Change.

Zamin, T. J., and P. Grogan. 2012. Birch shrub growth in the low Arctic: the relative importance of experimental warming, enhanced nutrient availability, snow depth and caribou exclusion. Environmental Research Letters 7:034027.

Zeng, H., G. Jia, and H. Epstein. 2011. Recent changes in phenology over the northern high latitudes detected from multi-satellite data. Environmental Research Letters 6:045508.

Figure captions

Figure 1. Ecological monitoring parameters from the Qikiqtaruk monitoring program (Cooley et al. 2012) following the protocols of the International Tundra Experiment (Molau and Mølgaard 1996).

Figure 2. The location of Qikiqtaruk within the circumpolar Arctic (a and b) and the location of the phenology, community composition, and permafrost monitoring sites on Qikiqtaruk (c). The landscape context is indicated by true color and normalized difference vegetation indices (NDVI) maps of the community composition plots (d). The Herschel vegetation type plots are indicated in blue, the Komaukuk vegetation type are indicated in yellow and the Orca floodplain vegetation type are indicated in green (see also figures below). Stars indicate phenocams at the community composition plots (d). The red dot indicates the location of the Herschel Island Environment Canada Weather Station. Image data were obtained in the summer of 2016 with Sony α6000 and MicaSense Sequoia cameras carried on multirotor drone platforms, and analyzed with image-based modelling approaches to yield digital orthomosaics with spatial grains of 0.05 m.

Figure 3. Temperatures are warming (a-d), frost frequency is decreasing (e), the snow melt data is getting earlier (f), sea ice concentrations are lower (g) and soil temperatures are warming (h) on Qikiqtaruk. Changes in climate and environmental data from Qikiqtaruk including air temperatures (a – d, Environment Canada data), frost day frequency (e, number of frost days, CRU TS3.21 data), snow melt date (f, phenology monitoring), sea ice concentration (g, Canadian Sea Ice Service data for the CIS WA Beaufort Sea: Mackenzie region), and soil temperature at 12, 15 and 16 m depths from two different boreholes (h, soil temperature monitoring data). Three records with outlier values were not included in the models in plot h for the years 2007 and 2012. Air temperature plots show mean values

for the months indicated. Trends lines are Bayesian model fits with error of 95% credible intervals. Full model outputs can be found in Table S2.

Figure 4. Active layer depth is increasing on Qikiqtaruk (a) across years and (b) mean active layer depth across the growing season in 2017 are lower in the Komakuk (blue) versus Herschel (yellow) vegetation types. The data from 1985 are from Smith et al. 1989, 2003-2007 data are from Burn and Zhang 2009, 2007-2008 data are data collection for snow fence data from the ArcticWOLVES project (S Gilbert, D Reid, CJ Krebs and IH Myers-Smith, unpublished data). The 2016-2017 data were collected by the Qikiqtaruk ecological monitoring team. Points show mean active layer depth and error bars show minimum and maximum active layer depth recorded at each site for (a) and each plot for (b).

Figure 5. Repeat photography indicates increases in tall shrubs in the Orca flood plain vegetation type from the East Ice Creek catchment on Qikiqtaruk from 1987 through 2017 (Myers-Smith et al. 2011b). The dominant shrub species in the photograph is *Salix richardsonii* which has reached a canopy height of over a meter in the foreground of the images by 2017. Photographs were taken in the second half of July in 2009-2017 and likely in early July in 1987. Similar increases are shown in photographs from another location on the floodplain farther from the creek bed (IH Myers-Smith, unpublished data). Repeat photography is now complemented by phenocam and drone observations at this and other ecological monitoring sites allowing for changes to be captured across the landscape.

Figure 6. Spring plant phenology including leaf emergence (a) and flowering (b) is earlier and leaf senescence has also advanced (c) leading to no substantial increase in realized growing season length for the species *Salix arctica* (d). Note that *Eriophorum vaginatum* monitoring did not start until 2002 and we did not model 2001 for Salix arctica senescence (P5) because there was only one data point

collected. Data points are the midpoint between the lower and upper bounds of the raw phenological observation data for each plot in a given year, errors are 95% credible intervals. Green indicates records for the willow species *Salix arctica*, purple for the flowering shrub species *Dryas integrifolia* and orange for the tussock sedge species *Eriophorum vaginatum*. Full model outputs can be found in Table S2.

Figure 7. Plot canopies are increasing in the Komakuk (blue) and Herschel (yellow) vegetation types (a), with species-specific canopy height increasing for the tall willow shrub *Salix pulchra* (green, b), yet high temporal variation indicated for *Salix* spp. radial growth (c). Trends lines are Bayesian model fits with error of 95% credible intervals. Full model outputs can be found in Table S2.

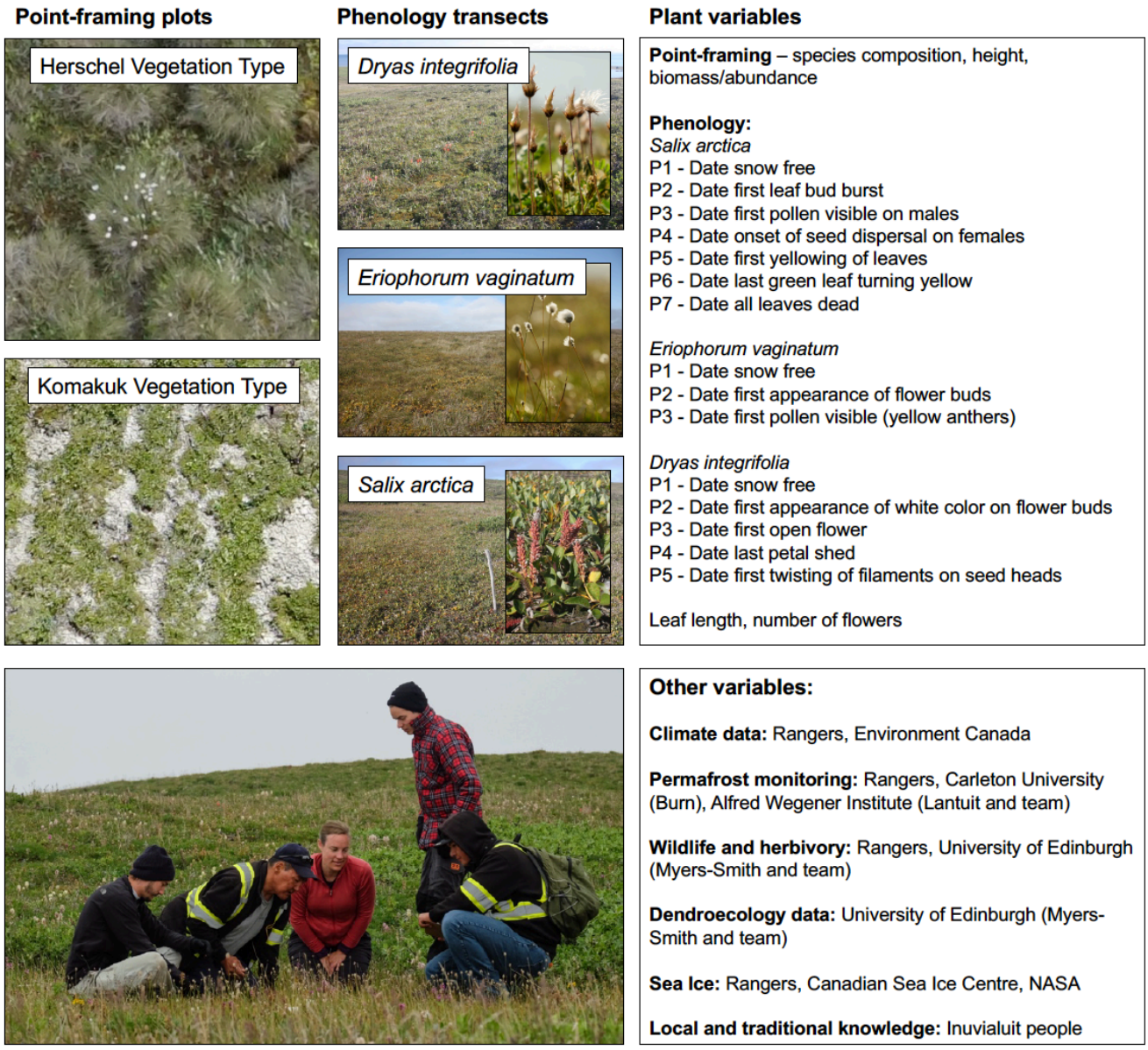
Figure 8. Vegetation cover (a) is increasing and bare ground (b) is decreasing in the Komakuk (blue) and Herschel (yellow) vegetation types from 1999-2017. Diversity metrics including species richness (c) and evenness (d) have not undergone substantial change. However, increases have occurred for the sedge species *Eriophorum vaginatum* (orange), the shrub species *Salix pulchra* (green) in the Herschel vegetation type (e) and the two grass species *Alopercurus alpinus* (light yellow) and *Arctagrostis latifolia* (light blue) in the Komakuk vegetation type (f). Trends lines are Bayesian model fits with error of 95% credible intervals. Full model outputs can be found in Table S2 and results for trends in cover of all species in the Herschel and Komakuk in Tables S3 and S4 respectively.

Figure 9. Future increases in species richness could occur due to the proximity of species not presently found within the long-term ecological monitoring plots. Vascular plant species accumulation curves for the Herschel and Komakuk vegetation communities on Qikiqtaruk. Smooth curves were fit using the loess method. Distance refers to distance away from the center of the community composition plots on

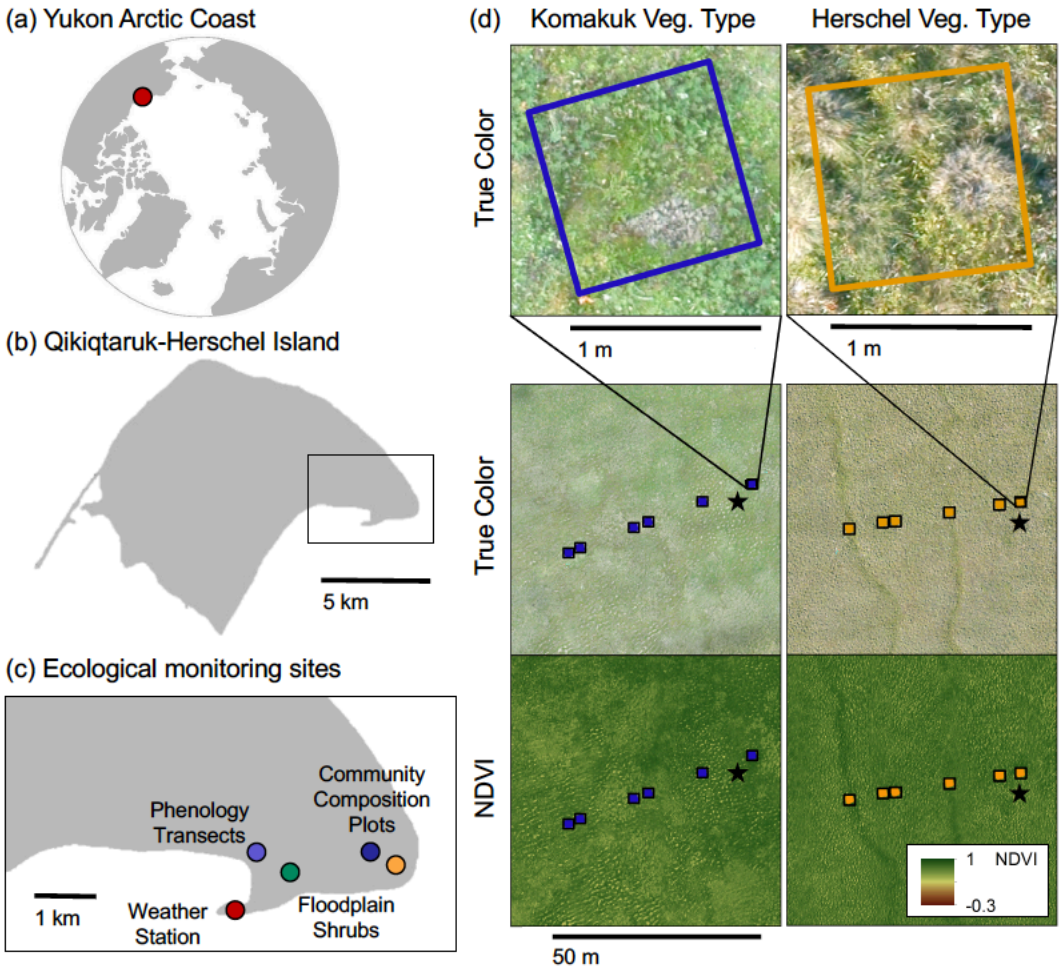
Collinson Head. Photographs illustrate the vascular plant species that have invaded the Komakuk plots, *Alopecurus alpinus*, and the four closest species growing within 5m of the Herschel and Komakuk vegetation types in 2017.

Figure 10. The relative strength of the relationships between environmental and ecological drivers and response parameters over time on Qikiqtaruk (a; effect sizes from Figures 3 – 8) and a simplified summary of the likely mechanisms by which vegetation change on Qikiqtaruk occurs (b). The standardized slope coefficients and credible intervals (slope coefficients or credible intervals divided by the standard deviation of the data) for models of all the monitored parameters in this study indicate weak increases in temperatures over the monitoring period, but stronger changes in active layer depths. Vegetation responses are variable, but indicate strong increases in vegetation cover and canopy height, decreases in bare ground and ring widths, and earlier leaf emergence, senescence, and flowering for monitored plant species. Vegetation change parameters not directly measured that may also be changing are shrub axial growth rates and stem numbers (Figure 7). Colors indicate the category of variable and correspond to the variable colors in the previous figures. Red indicates temperature variables, blue indicates variables associated with freezing temperatures, snow melt, sea ice and permafrost, the other colors indicate the different plant species and vegetation communities (see above figure captions). Frost days are calculated from temperature data, yet represent a variable associated with ice-y conditions and are thus indicated in blue, yet in the temperature category.

Figure 1. (Box 1)

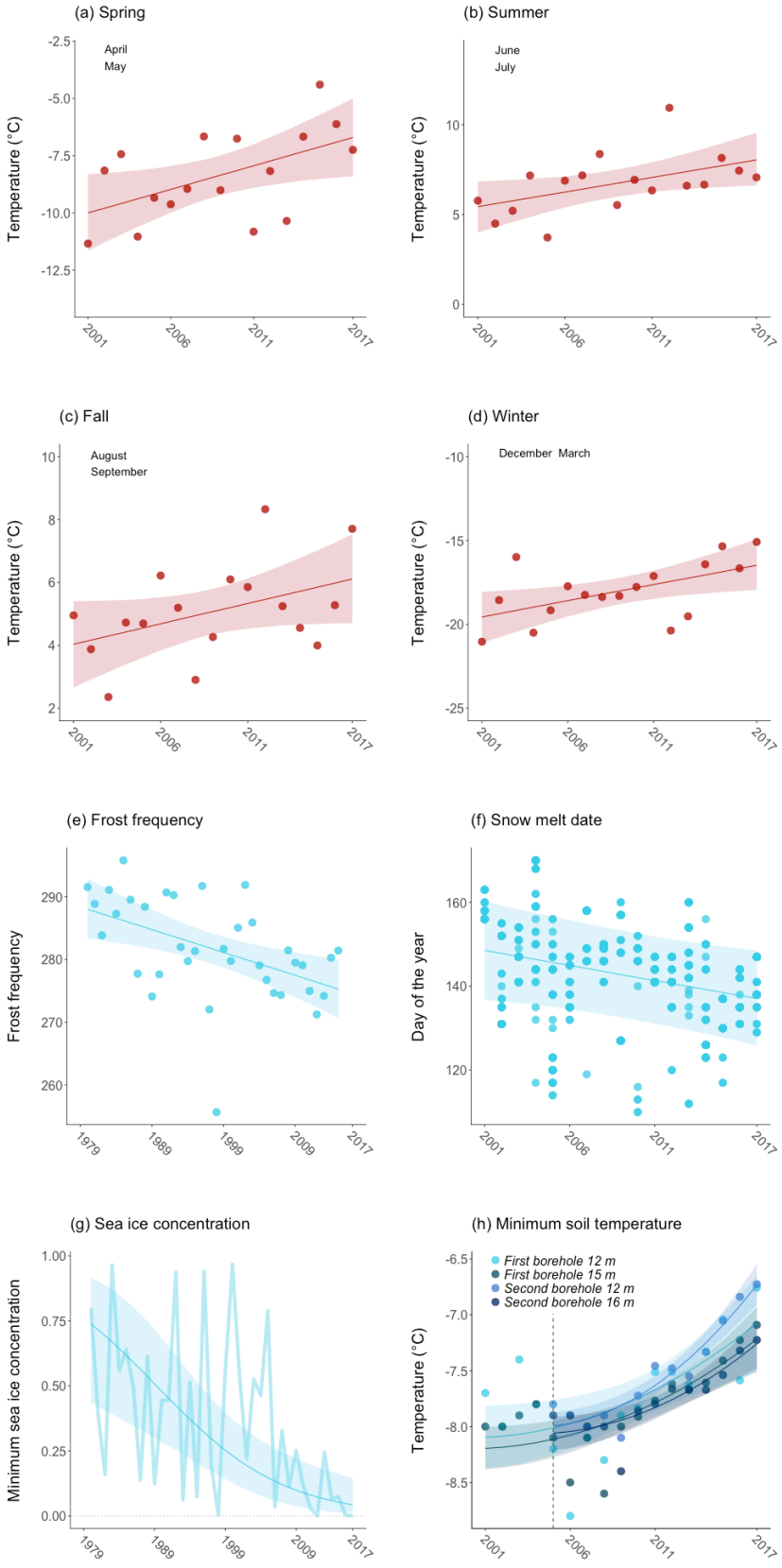


1122 Figure 2.



1123

1124 Figure 3.



1125

Figure 4.

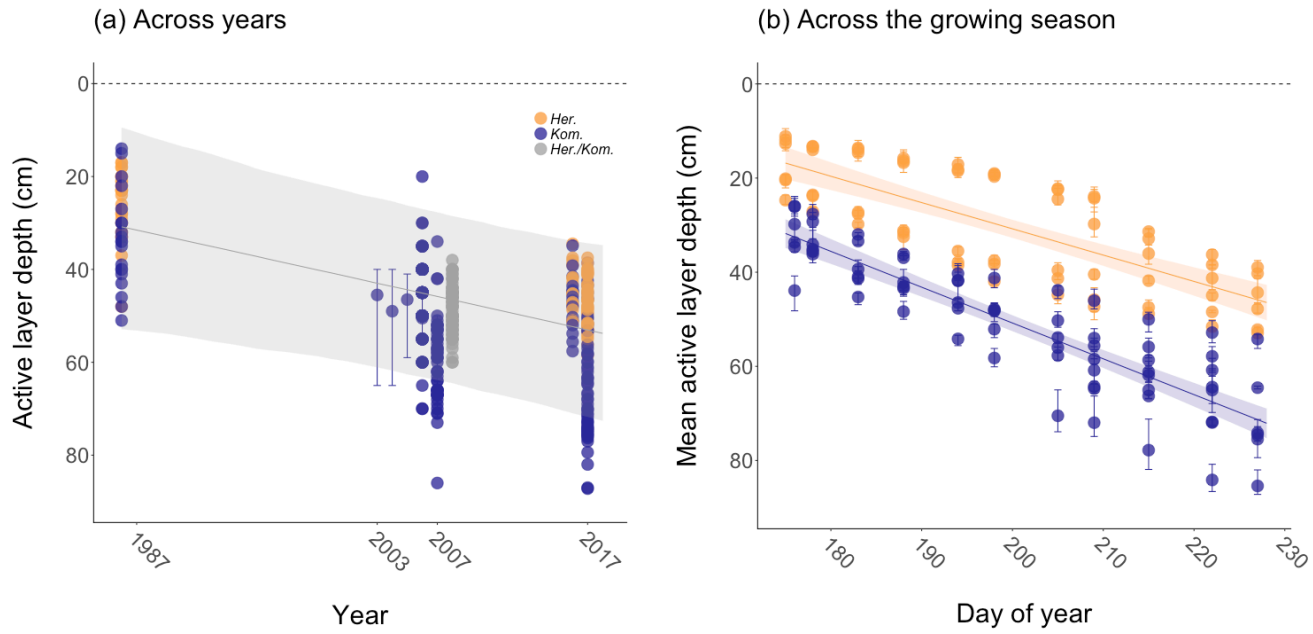

(a) Across years
Active layer depth (cm)
0
20
40
60
80
1987
2003
2007
2017
Year
Her.
Kom.
Her./Kom.
(b) Across the growing season
Mean active layer depth (cm)
0
20
40
60
80
180
190
200
210
220
230
Day of year

Figure 5.

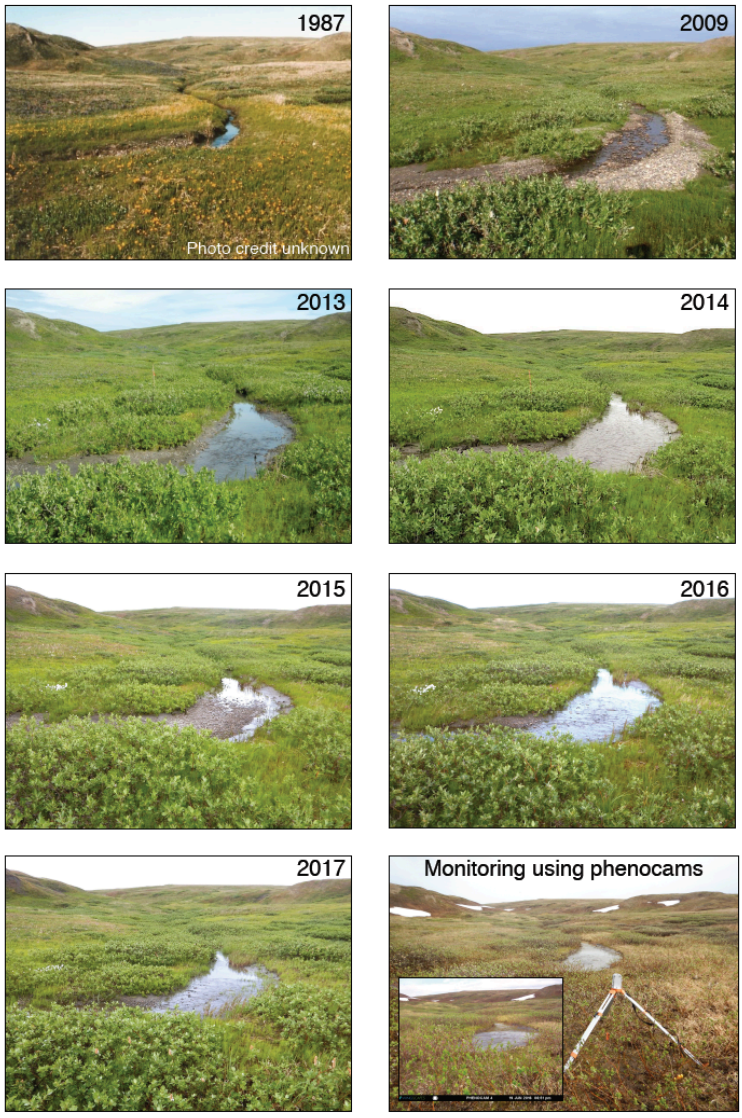

1987
Photo credit unknown
2009
2013
2014
2015
2016
2017
Monitoring using phenocams

Figure 6.

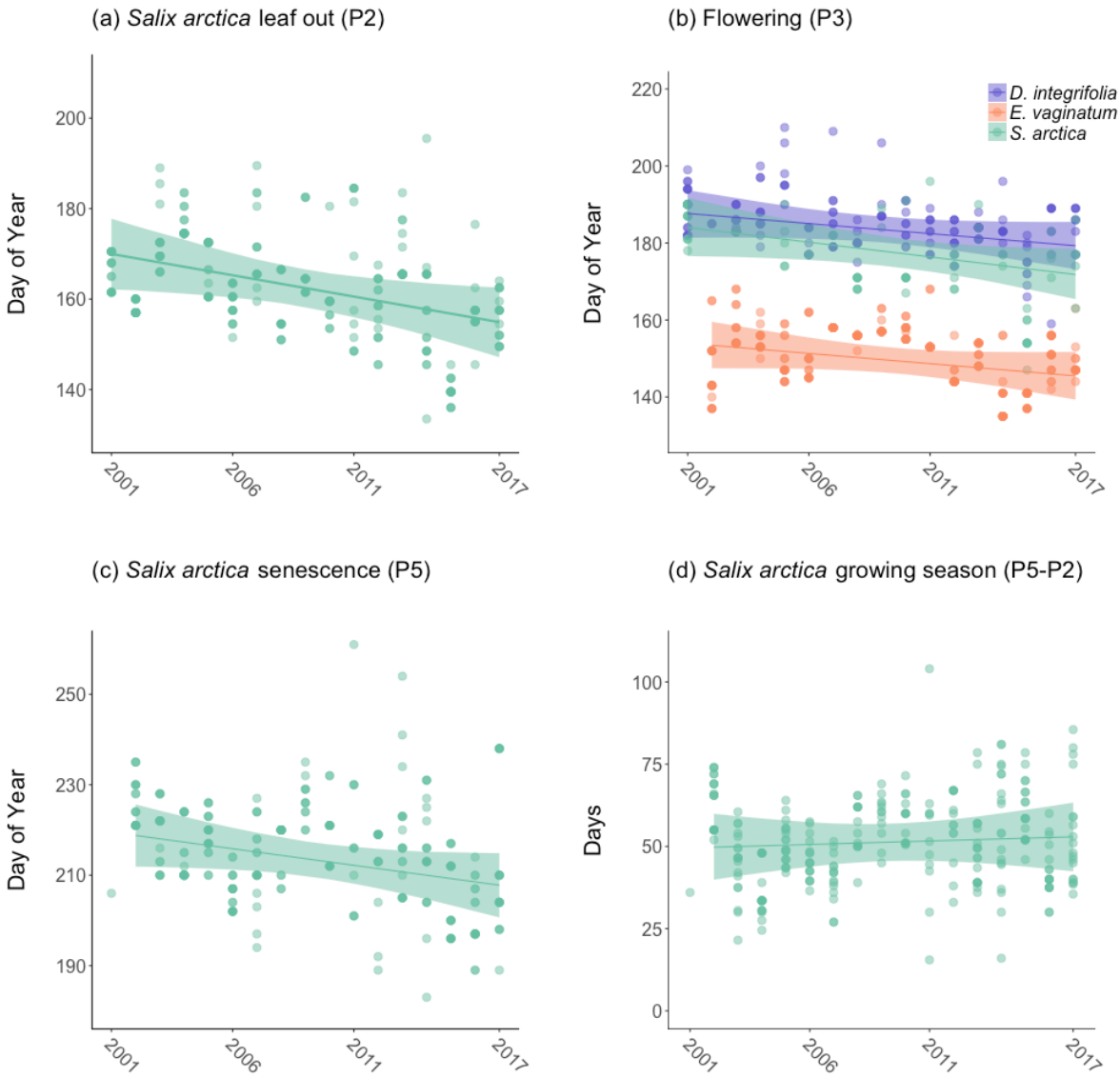

(a) Salix arctica leaf out (P2)
Day of Year
200
180
160
140
2001
2006
2011
2017
(b) Flowering (P3)
D. integrifolia
E. vaginatum
S. arctica
Day of Year
220
200
180
160
140
2001
2006
2011
2017
(c) Salix arctica senescence (P5)
Day of Year
250
230
210
190
2001
2006
2011
2017
(d) Salix arctica growing season (P5-P2)
Days
100
75
50
25
0
2001
2006
2011
2017

Figure 7.

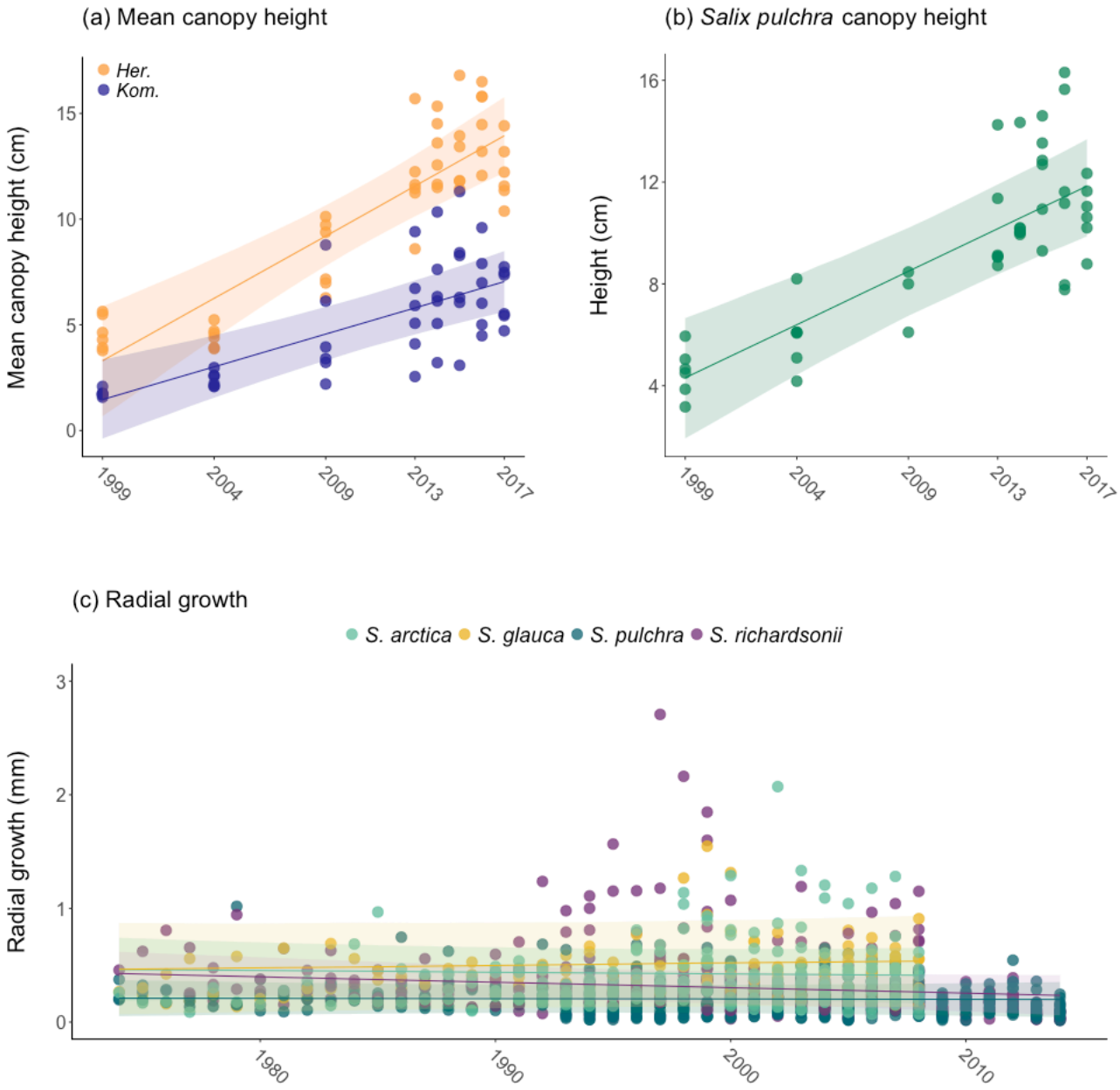
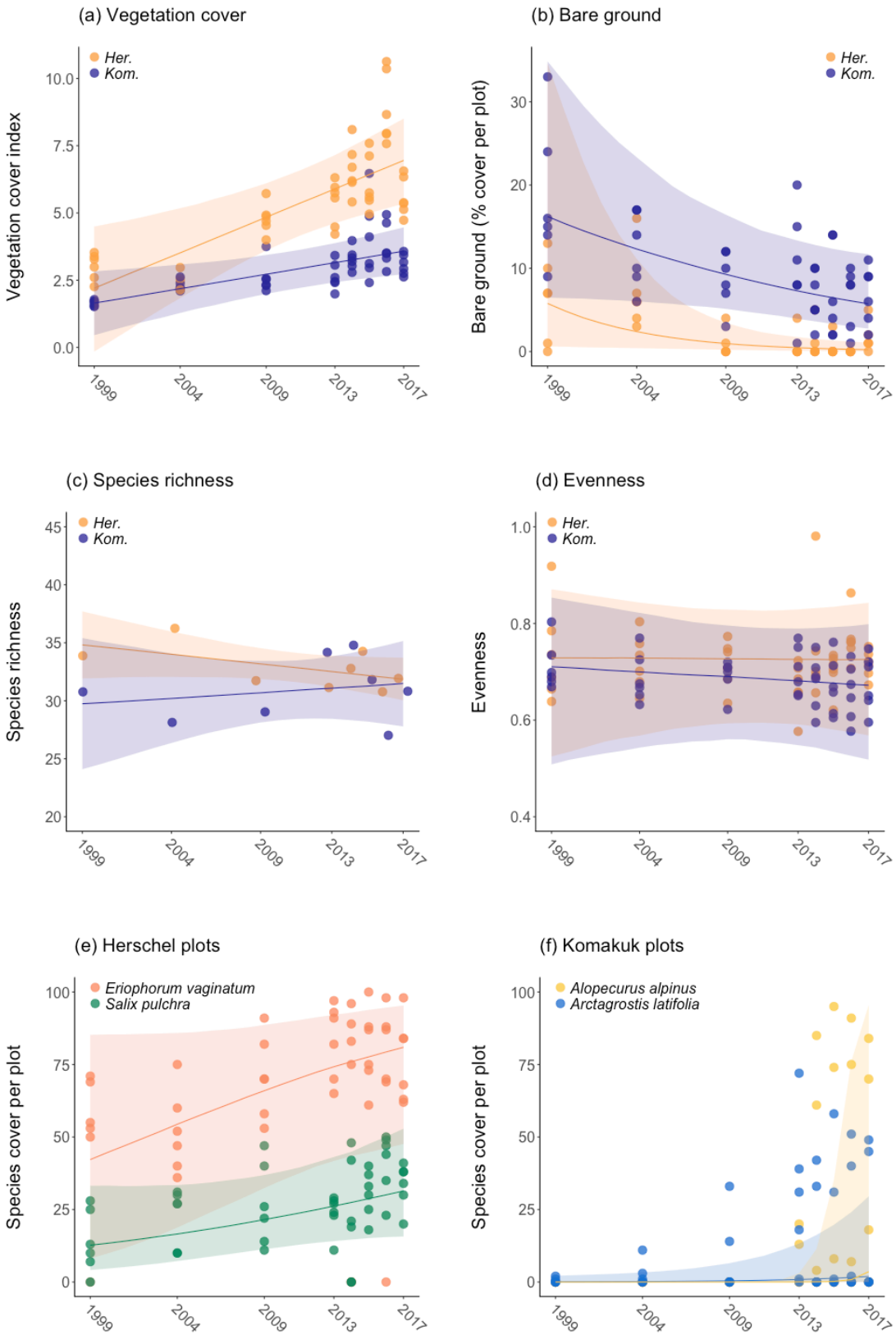
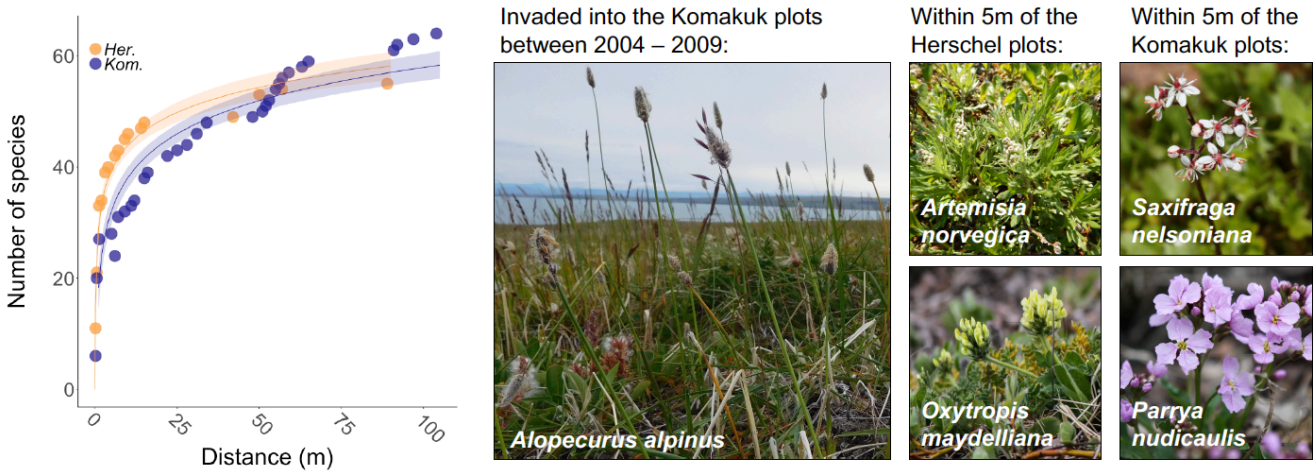

(a) Mean canopy height
Her.
Kom.
Mean canopy height (cm)
0
5
10
15
1999
2004
2009
2013
2017
(b) Salix pulchra canopy height
Height (cm)
4
8
12
16
1999
2004
2009
2013
2017
(c) Radial growth
S. arctica
S. glauca
S. pulchra
S. richardsonii
Radial growth (mm)
0
1
2
3
1980
1990
2000
2010

Figure 8.

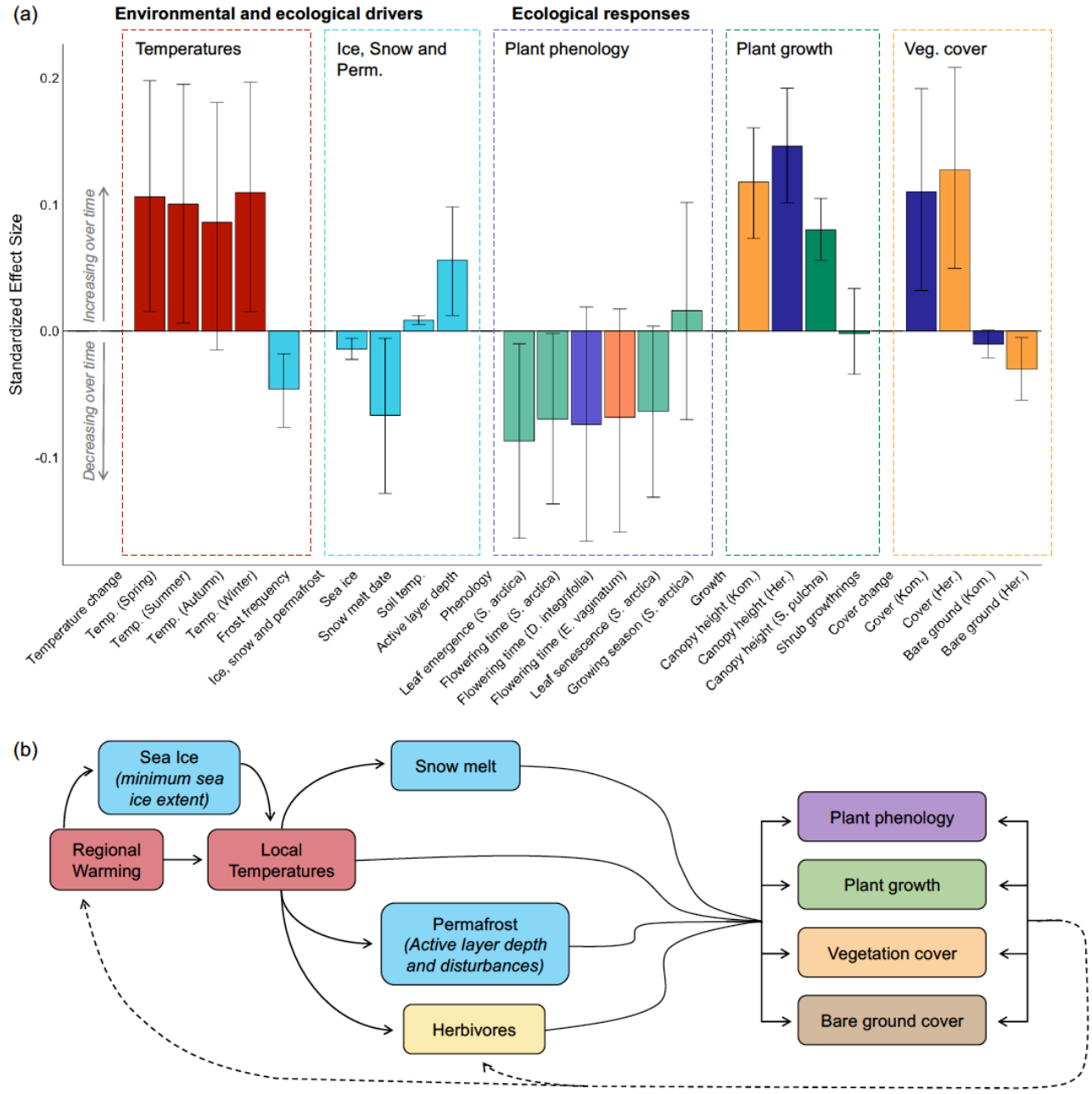

(a) Vegetation cover
Vegetation cover index
Her.
Kom.
(b) Bare ground
Bare ground (% cover per plot)
(c) Species richness
Species richness
(d) Evenness
Evenness
(e) Herschel plots
Species cover per plot
Eriophorum vaginatum
Salix pulchra
(f) Komakuk plots
Alopecurus alpinus
Arctagrostis latifolia
1999
2004
2009
2013
2017

1136 Figure 9.



1137

1138 Figure 10.



1139

Supporting information

Table S1. Formulas for converting resistance values (Ω) from the two boreholes on Qikiqtaruk-Herschel Island into soil temperature values (°C).

Depth (m)	Correction
12 m – first borehole	Resistance (Ω) + 12
15 m – first borehole	Resistance (Ω) - 39
12 m – second borehole	Resistance (Ω) + 18
16 m – second borehole	Resistance (Ω) - 18
Beta (Excel formula)	=IF(RESISTANCE<3539,99.99,IF(RESISTANCE<4483,(LOG(3539/4483))/((1/288.15)-(1/283.15)),IF(RESISTANCE<5720,(LOG(4483/5720))/((1/283.15)-(1/278.15)),IF(RESISTANCE<7355,(LOG(5720/7355))/((1/278.15)-(1/273.15)),IF(RESISTANCE<9533,(LOG(7355/9533))/((1/273.15)-(1/268.15)),IF(RESISTANCE<12460,(LOG(9533/12460))/((1/268.15)-(1/263.15)),99.99))))))
Conversion formula (Excel formula)	=IF(RESISTANCE<3539,99.99,IF(RESISTANCE<4483,(BETA/(LOG(RESISTANCE/4483)+BETA/283.15))-273.15,IF(RESISTANCE<5720,(BETA/(LOG(RESISTANCE/4483)+BETA/283.15))-273.15,IF(RESISTANCE<7355,BETA/((LOG(RESISTANCE/5720)+BETA/278.15))-273.15,IF(RESISTANCE<9533,BETA/((LOG(RESISTANCE/7355)+BETA/273.15))-273.15,IF(RESISTANCE<12460,BETA/((LOG(RESISTANCE/9533)+BETA/268.15))-273.15,99.99))))))

Table S2. All model results for Bayesian models. Sigma is the overall model residual variance and the year and plot sigma values are labelled with a residual versus fixed effect type. P-values are only provided for the MCMCglmm models.

Model name	Model type	Variable	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	pMCMC	Effect type
Spring temperature	Linear	(Intercept)	-10.19	-12.07	-8.35	8000	<0.01	fixed
		Year	0.2	0.02	0.38	8000	0.03	fixed
		Sigma	3.37	1.28	6.09	8000	-	residual
Summer temperature	Linear	(Intercept)	5.26	3.7	6.85	8000	<0.01	fixed
		Year	0.16	0.01	0.31	8000	0.04	fixed
		Sigma	2.44	0.98	4.52	8000	-	residual
Autumn temperature	Linear	(Intercept)	3.9	2.4	5.42	8000	<0.01	fixed
		Year	0.13	-0.01	0.28	8000	0.09	fixed
		Sigma	2.27	0.9	4.16	8000	-	residual
Winter temperature	Linear	(Intercept)	-19.76	-21.36	-18.1	7953	<0.01	fixed
		Year	0.19	0.03	0.35	8000	0.02	fixed
		Sigma	2.69	0.97	4.85	8000	-	residual
Frost frequency	Linear	(Intercept)	288.39	283.5	293.27	8000	<0.01	fixed
		Year	-0.36	-0.58	-0.12	8272	<0.01	fixed
		Sigma	52.78	29.35	79.37	8000	-	residual
Snow melt days	Linear	(Intercept)	149.17	136.8	160.85	8273	<0.01	fixed
		Year	-0.71	-1.37	-0.05	8000	0.04	fixed
		Sigma	38.84	35.4	42.43	8000	-	residual
Sea ice concentration	Binomial	(Intercept)	1.16	-0.24	2.52	7601	0.09	fixed
		Year	-0.11	-0.17	-0.05	7264	<0.01	fixed
		Sigma	4.39	2.26	6.94	6503	-	residual
Soil temperature at 12 m depth (first borehole)	Linear	(Intercept)	-8.10	-8.40	-7.83	7121	<0.01	fixed
		Year (squared)	0.004	0.003	0.006	8000	0.002	fixed
		Sigma	0.06	0.04	0.08	8000	-	residual
Soil temperature at 15 m depth (first borehole)	Linear	(Intercept)	-8.20	-8.39	-8.01	8272	<0.01	fixed

		Year (squared)	0.003	0.002	0.005	8000	<0.01	fixed
		Sigma	0.07	0.03	0.12	8000	-	residual
Soil temperature at 12 m depth (second borehole)	Linear	(Intercept)	-8.00	-8.13	-7.88	7708	<0.01	fixed
		Year (squared)	0.008	0.006	0.009	8000	<0.01	fixed
		Sigma	0.02	0.01	0.05	8000	-	residual
Soil temperature at 16 m depth (second borehole)	Linear	(Intercept)	-8.07	-8.22	-7.92	7560	<0.01	fixed
		Year (squared)	0.005	0.003	0.007	8000	<0.01	fixed
		Sigma	0.03	0.01	0.06	8000	-	residual
Active layer depth across 1985-2017	Linear	(Intercept)	30.16	9.98	53.93	8000	0.02	fixed
		Year	0.72	0.21	1.29	7848	0.02	fixed
		Sigma	66.2	57.35	75.5	8000	-	residual
Active layer depth across the 2017 growing season (Herschel)	Linear	(Intercept)	16.22	12.75	19.74	8000	<0.01	fixed
		Day	0.56	0.45	0.67	7786	<0.01	fixed
		Sigma	64.06	43.02	87.95	9066	-	residual
Active layer depth across the 2017 growing season (Komakuk)	Linear	(Intercept)	30.98	27.88	34.06	7961	<0.01	fixed
		Day	0.76	0.66	0.86	8000	<0.01	fixed
		Sigma	50.19	34.48	67.24	7649	-	residual
Leaf out (P2) *S. arctica*	Linear interval censoring	(Intercept)	170.69	162.42	178.97	6000	-	fixed
		Year	-0.93	-1.69	-0.12	4300	-	fixed
		Sigma-Year	7.86	5.34	11.93	6000	-	random
		Sigma-Plot	2.98	1.82	4.55	3900	-	random
		Sigma-Resid	6.37	5.86	6.93	6000	-	random

Flowering (P3)	Linear interval censoring							
D. integrifolia		(Intercept)	188.28	181.56	195.13	6000	-	fixed
		Year	-0.53	-1.18	0.13	6000	-	fixed
E. vaginatum		(Intercept)	154.56	147.14	162.34	3800	-	fixed
		Year	-0.54	-1.27	0.15	5800	-	fixed
S. arctica		(Intercept)	184.67	176.43	192.97	4000	-	fixed
		Year	-0.75	-1.52	0.02	5700	-	fixed
		Sigma-Year	6.39	4.98	8.13	3300	-	random
		Sigma-Plot	1.78	1.13	2.59	2200	-	random
		Sigma-Resid	4.83	4.51	5.17	6000	-	random
Senescence (P5) *S. arctica*	Linear interval censoring	(Intercept)	219.6	211.92	227.37	6000	-	fixed
		Year	-0.74	-1.53	0.03	6000	-	fixed
		Sigma-Year	6.9	4.44	10.73	5500	-	random
		Sigma-Plot	2.34	0.57	4.36	900	-	random
		Sigma-Resid	9.11	8.31	10.02	3500	-	random
Growing season length (slope difference P5-P2)	Linear interval censoring	Year	0.21	-0.92	1.36	6300	-	derived
Canopy height (Herschel)	Linear	(Intercept)	2.69	-0.07	5.29	8000	0.05	fixed
		Year	0.59	0.42	0.79	8000	<0.01	fixed
		Year	2.1	0.21	5.19	8000	-	random
		Plot	1.01	0.08	2.72	8305	-	random
		Sigma	2.14	1.18	3.19	8000	-	residual
Canopy height (Komakuk)	Linear	(Intercept)	1.14	-0.74	3.1	8000	0.22	fixed
		Year	0.31	0.2	0.43	8000	<0.01	fixed
		Year	0.53	0.07	1.35	8000	-	random
		Plot	1.61	0.11	4.4	8000	-	random
		Sigma	2.7	1.57	3.93	8000	-	residual
Canopy height (*S. pulchra*)	Linear	(Intercept)	3.89	1.42	6.34	8000	<0.01	fixed
		Year	0.42	0.29	0.55	8000	<0.01	fixed
		Year	0.98	0.12	2.48	8000	-	random
		Plot	3.6	0.53	9.04	8000	-	random
		Sigma	20.6	18.99	22.37	8000	-	residual
Radial growth (*S. richardsonii*)	Linear	(Intercept)	0.43	0.24	0.63	8000	<0.01	fixed
		Year	0	-0.01	0	8294	0.11	fixed

		Year	0.04	0.02	0.05	8974	-	random
		Individual	0.09	0.05	0.16	8000	-	random
		Sigma	0.04	0.03	0.04	8000	-	residual
Radial growth (*S. pulchra*)	Linear	(Intercept)	0.21	0.05	0.37	8000	0.01	fixed
		Year	0	-0.01	0	8000	0.91	fixed
		Year	0.03	0.02	0.05	8645	-	random
		Individual	0.06	0.03	0.1	8000	-	random
		Sigma	0.01	0.01	0.01	8000	-	residual
Radial growth (*S. arctica*)	Linear	(Intercept)	0.46	0.18	0.76	8000	<0.01	fixed
		Year	0	-0.01	0.01	8000	0.73	fixed
		Year	0.05	0.02	0.07	7267	-	random
		Individual	0.16	0.06	0.29	8000	-	random
		Sigma	0.03	0.03	0.04	8000	-	residual
Radial growth (*S. glauca*)	Linear	(Intercept)	0.47	0.08	0.89	8000	0.03	fixed
		Year	0	-0.01	0.01	8000	0.61	fixed
		Year	0.05	0.03	0.07	8000	-	random
		Individual	0.23	0.05	0.54	8000	-	random
		Sigma	0.04	0.03	0.05	8000	-	residual
Vegetation cover (Herschel)	Binomial	(Intercept)	1.96	-0.48	4.38	8000	0.11	fixed
		Year	0.26	0.09	0.42	8000	0.01	fixed
		Year	1.93	0.35	4.73	8468	-	random
		Plot	0.69	0.09	1.77	8000	-	random
		Sigma	0.42	0.24	0.64	8000	-	residual
Vegetation cover (Komakuk)	Binomial	(Intercept)	1.54	0.23	2.74	8519	0.02	fixed
		Year	0.11	0.03	0.19	8000	0.02	fixed
		Year	0.4	0.07	0.99	8000	-	random
		Plot	0.44	0.06	1.1	7912	-	random
		Sigma	0.4	0.23	0.6	8000	-	residual
Bare ground (Herschel)	Binomial	(Intercept)	-2.64	-5.06	-0.28	5269	0.04	fixed
		Year	-0.18	-0.35	-0.02	1365	0.02	fixed
		Year	1.59	0.11	4.62	102	-	random
		Plot	1.37	0.15	3.68	4655	-	random
		Sigma	0.35	0	1.03	302	-	residual
Bare ground (Komakuk)	Binomial	(Intercept)	-1.56	-2.62	-0.47	8000	0.01	fixed
		Year	-0.07	-0.13	0	8000	0.06	fixed
		Year	0.28	0.05	0.67	7640	-	random
		Plot	0.35	0.06	0.86	8000	-	random
		Sigma	0.27	0.09	0.48	4978	-	residual

Species richness (Herschel)	Binomial	(Intercept)	35.01	32.09	37.97	8000	<0.01	fixed
		Year	-0.17	-0.38	0.04	8000	0.11	fixed
		Sigma	3.22	0.56	7.8	8000	-	residual
Species richness (Komakuk)	Binomial	(Intercept)	29.63	23.94	35.85	8318	<0.01	fixed
		Year	0.1	-0.34	0.52	8282	0.61	fixed
		Sigma	12.98	2.17	31.49	7590	-	residual
Evenness (Herschel)	Binomial	(Intercept)	0.99	0	1.92	8000	0.05	fixed
		Year	0	-0.06	0.06	8000	0.96	fixed
		Year	0.24	0.05	0.55	7992	-	random
		Plot	0.34	0.06	0.87	8000	-	random
		Sigma	0.02	0	0.05	792	-	residual
Evenness (Komakuk)	Binomial	(Intercept)	0.89	-0.04	1.74	8000	0.05	fixed
		Year	-0.01	-0.06	0.05	6398	0.72	fixed
		Year	0.21	0.04	0.49	8413	-	random
		Plot	0.28	0.05	0.69	8000	-	random
		Sigma	0.01	0	0.02	972	-	residual
E. vaginatum cover (Herschel)	Binomial	(Intercept)	-0.43	-2.68	1.62	8000	0.68	fixed
		Year	0.1	-0.03	0.23	8000	0.12	fixed
		Year	0.71	0.08	1.88	7646	-	random
		Plot	1.94	0.17	5.37	7604	-	random
		Sigma	2.65	1.23	4.23	5117	-	residual
S. pulchra cover (Herschel)	Binomial	(Intercept)	-1.99	-3.31	-0.73	8000	<0.01	fixed
		Year	0.06	-0.02	0.14	8000	0.11	fixed
		Year	0.4	0.06	0.98	6735	-	random
		Plot	0.48	0.07	1.23	8000	-	random
		Sigma	0.48	0.2	0.84	5909	-	residual
A. latifolia cover (Komakuk)	Binomial	(Intercept)	-7.81	-11.97	-3.51	4799	<0.01	fixed
		Year	0.2	-0.01	0.41	5411	0.06	fixed
		Year	1.5	0.07	4.24	7037	-	random
		Plot	11.5	1.18	29.83	6959	-	random
		Sigma	4.55	1.59	8.94	2125	-	residual
A. alpinus (Komakuk)	Binomial	(Intercept)	-32.1	-52.69	-15.03	115	<0.01	fixed
		Year	1.5	0.64	2.61	110	<0.01	fixed
		Year	1.93	0.07	6.62	1335	-	random
		Plot	52.72	0.21	165.86	482	-	random
		Sigma	14.63	3.29	31.87	453	-	residual

Species pool (Herschel)	Linear	(Intercept)	28.9	26.88	31.11	7639	<0.01	fixed
		log(Distance)	6.5	5.7	7.32	7682	<0.01	fixed
		Sigma	8.07	3.07	14.95	8000	-	residual
Species pool (Komakuk)	Linear	(Intercept)	18.23	14.4	21.76	8000	<0.01	fixed
		log(Distance)	8.61	7.53	9.72	8000	<0.01	fixed
		Sigma	22.71	12.21	35.9	8000	-	residual

1147

Table S3. Trends in species cover over time for the Herschel Vegetation Type. Model results for a Bayesian linear model of cover change with year by species interaction and plot and year as a random effects. The slope estimates and significance tests are only approximate as the linear model does not capture the fact that percent cover data are bounded between 0 and 1 and are zero inflated. More complex modelling structures had poor convergence.

Species	Approx. cover change over time (% cover/year)	Lower 95% CI	Upper 95% CI	Effective sample size	pMCMC	Effect type
Alopecurus alpinus	-0.02	-0.36	0.35	8000	0.95	fixed
Arctagrostis latifolia	0.57	0.22	0.93	8000	0	fixed
Astragalus umbellatus	-0.01	-0.38	0.35	8000	0.94	fixed
Cardamine bellidifolia	-0.01	-0.37	0.36	8178	0.96	fixed
Cardamine digitalis	0.06	-0.29	0.42	8000	0.76	fixed
Carex sp.	0.26	-0.09	0.63	8000	0.15	fixed
Cassiope tetragona	-0.03	-0.4	0.33	8000	0.85	fixed
Cetraria cucculata	-0.2	-0.57	0.16	8000	0.28	fixed
Cetraria islandica	-0.16	-0.53	0.19	8000	0.39	fixed
Cetraria nivalis	-0.01	-0.38	0.34	8000	0.96	fixed
Cladina (brown)	-0.02	-0.37	0.36	8000	0.94	fixed
Cladina mitis	0	-0.38	0.34	8000	0.98	fixed
Dactylina arctica	-0.04	-0.39	0.33	8000	0.83	fixed
Dryas integrifolia	-0.08	-0.44	0.28	8000	0.69	fixed
Eriophorum angustifolium	0.17	-0.19	0.53	8000	0.37	fixed
Eriophorum vaginatum	1.49	1.11	1.83	8000	0	fixed
Festuca baffinensis	0.02	-0.32	0.4	8000	0.9	fixed
Hierochloe alpine	-0.02	-0.37	0.36	8000	0.91	fixed
Kobresia myosuroides	0	-0.37	0.36	8316	0.98	fixed
Kobresia sibirica	-0.01	-0.36	0.36	8000	0.96	fixed
Lagotis glauca	0	-0.38	0.35	8000	0.99	fixed
Lupinus arcticus	-0.04	-0.41	0.31	8000	0.82	fixed
Luzula arctica	0.09	-0.26	0.45	7292	0.65	fixed
Oxytropis	-0.02	-0.39	0.33	8000	0.93	fixed
Oxytropis campestris	-0.01	-0.38	0.33	8000	0.94	fixed
Oxytropis maydelliana	-0.01	-0.37	0.35	8450	0.94	fixed
Oxytropis nigrescens	-0.02	-0.39	0.35	8000	0.93	fixed
Papaver radicatum	-0.01	-0.37	0.37	8000	0.94	fixed
Parrya nudicaulis	-0.01	-0.36	0.35	8000	0.94	fixed
Pedicularis	-0.01	-0.38	0.33	8000	0.94	fixed
Pedicularis capitata	0.01	-0.34	0.37	8474	0.96	fixed
Pedicularis lanata	-0.05	-0.42	0.32	8000	0.8	fixed
Pedicularis sudetica	-0.03	-0.37	0.36	8459	0.89	fixed
Pedicularis vertisilata	-0.01	-0.38	0.35	8000	0.96	fixed
Poa alpina	-0.01	-0.37	0.36	8000	0.93	fixed
Poa arctica	0.45	0.09	0.81	8000	0.01	fixed

Polygonum bistorta	0.11	-0.26	0.46	8402	0.55	fixed
Polygonum viviparum	-0.02	-0.38	0.35	9076	0.91	fixed
Pyrola grandiflora	-0.02	-0.38	0.35	8405	0.91	fixed
Salix arctica	-0.04	-0.39	0.33	8000	0.84	fixed
Salix phlebophylla	0.02	-0.33	0.39	8000	0.91	fixed
Salix pulchra	1	0.63	1.36	8000	0	fixed
Salix reticulata	0.16	-0.22	0.51	8000	0.39	fixed
Saussurea angustifolia	-0.03	-0.39	0.34	8000	0.86	fixed
Saxifraga nelsoniana	0	-0.36	0.35	8000	0.98	fixed
Senecio atropurpureus	-0.04	-0.41	0.3	8000	0.8	fixed
Stellaria longipes	0.07	-0.3	0.43	8693	0.71	fixed
Thamnolia subuliformis	-0.15	-0.49	0.23	8000	0.44	fixed
Valeriana capitata	-0.01	-0.37	0.36	8000	0.95	fixed
Bareground	-0.13	-0.49	0.23	8000	0.49	fixed
Year	0.51	0.09	1.22	8000	-	random
Plot	0.39	0.06	1	8276	-	random
Sigma	29.76	28.3	31.17	8000	-	residual

1153

Table S4. Trends in species cover over time for the Komakuk Vegetation Type. Model results for a Bayesian linear model of cover change with year by species interaction and plot and year as a random effects. The slope estimates and significance tests are only approximate as the linear model does not capture the fact that percent cover data are bounded between 0 and 1 and are zero inflated. More complex modelling structures had poor convergence.

Species	Approx. cover change over time (% cover/year)	Lower 95% CI	Upper 95% CI	Effective sample size	pMCMC	Effect type
Alopecurus alpinus	1.84	1.49	2.16	8025	0	fixed
Arctagrostis latifolia	1	0.66	1.32	8000	0	fixed
Astragalus umbellatus	-0.03	-0.37	0.3	8000	0.89	fixed
Cardamine bellidifolia	-0.02	-0.36	0.32	8000	0.91	fixed
Cardamine digitalis	0.02	-0.33	0.36	8000	0.88	fixed
Cassiope tetragona	-0.03	-0.37	0.3	8000	0.88	fixed
Cetraria cucculata	-0.13	-0.48	0.2	8000	0.46	fixed
Cetraria islandica	-0.06	-0.41	0.27	7986	0.74	fixed
Cetraria nivalis	-0.03	-0.37	0.31	8344	0.88	fixed
Cladina (brown)	-0.02	-0.36	0.31	7488	0.9	fixed
Cladina mitis	0.01	-0.33	0.34	8000	0.95	fixed
Dactylina arctica	-0.02	-0.34	0.32	8000	0.9	fixed
Dryas integrifolia	0.28	-0.06	0.62	7311	0.1	fixed
Eriophorum angustifolium	-0.03	-0.36	0.31	8367	0.87	fixed
Eriophorum vaginatum	-0.03	-0.37	0.31	8000	0.88	fixed
Festuca baffinensis	0.02	-0.31	0.35	7819	0.88	fixed
Hierochloe alpine	-0.01	-0.35	0.33	8000	0.96	fixed
Kobresia myosuroides	-0.03	-0.36	0.3	8000	0.89	fixed
Kobresia sibirica	-0.03	-0.35	0.32	8000	0.88	fixed
Lagotis glauca	0	-0.35	0.33	8000	0.97	fixed
Lupinus arcticus	0.2	-0.14	0.54	8000	0.26	fixed
Luzula arctica	0.01	-0.31	0.38	8260	0.93	fixed
Oxytropis	-0.03	-0.35	0.32	8000	0.88	fixed
Oxytropis campestris	-0.01	-0.36	0.32	8000	0.95	fixed
Oxytropis maydelliana	0	-0.34	0.33	8000	0.98	fixed
Oxytropis nigrescens	-0.03	-0.38	0.3	7776	0.88	fixed
Papaver radicatum	-0.03	-0.39	0.29	8000	0.85	fixed
Parrya nudicaulis	-0.02	-0.37	0.31	8000	0.9	fixed
Pedicularis	-0.03	-0.36	0.32	8000	0.89	fixed
Pedicularis capitata	-0.02	-0.36	0.32	8000	0.92	fixed
Pedicularis lanata	-0.1	-0.43	0.25	8320	0.55	fixed

Pedicularis sudetica	-0.03	-0.35	0.32	8000	0.87	fixed
Pedicularis vertisilata	-0.01	-0.35	0.32	8000	0.97	fixed
Poa alpina	-0.03	-0.35	0.33	6963	0.89	fixed
Poa arctica	-0.08	-0.41	0.26	7528	0.64	fixed
Polygonum bistorta	0.01	-0.34	0.34	6929	0.97	fixed
Polygonum viviparum	0	-0.34	0.34	7342	0.97	fixed
Pyrola grandiflora	-0.03	-0.37	0.31	8000	0.87	fixed
Salix arctica	0.39	0.04	0.72	8000	0.03	fixed
Salix phlebophylla	-0.03	-0.37	0.29	8000	0.88	fixed
Salix pulchra	-0.02	-0.37	0.32	8000	0.89	fixed
Salix reticulata	-0.04	-0.38	0.29	8000	0.81	fixed
Saussurea angustifolia	-0.04	-0.38	0.29	8000	0.81	fixed
Saxifraga nelsoniana	-0.03	-0.39	0.3	8000	0.88	fixed
Senecio atropurpureus	-0.01	-0.34	0.34	8477	0.96	fixed
Stellaria longipes	-0.1	-0.46	0.22	7571	0.55	fixed
Thamnolia subuliformis	-0.13	-0.46	0.22	8000	0.45	fixed
Valeriana capitata	-0.03	-0.37	0.3	8332	0.87	fixed
Bareground	-0.04	-0.38	0.29	8000	0.81	fixed
Year	0.29	0.06	0.69	8294	-	random
Plot	0.32	0.04	0.79	8000	-	random
Sigma	25.34	24.16	26.55	7942	-	residual

1159