

RESEARCH ARTICLE

Increases in graminoids after three decades of change in the High Arctic

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Abstract

Climate change portends serious implications for Arctic vegetation. Understanding these effects is likely to be enhanced with long-term observations from permanent plots. I evaluated three decades of change in tundra vegetation from 80 permanent plots on south-eastern Victoria Island, Nunavut, Canada. I compared baseline (1991 and 1992) and contemporary (2019 and 2022) periods in the cover and frequency of graminoids, mosses and common species of forbs, shrubs and lichens. I found substantial shifts in cover of several species and growth forms—an increase in graminoids, decreases in *Dryas integrifolia*, *Polygonum viviparum* and *Saxifraga oppositifolia*, and marginally significant declines in mosses and *Cassiope tetragona*, but no detectable changes in other groups. The decline in *Dryas integrifolia* was more pronounced at lower elevations and was noticeable as patches of apparent mortality, inside the plots and elsewhere. The shifts in species abundance were not significantly correlated with each other, nor with changes in soil depth. These changes, manifest as communities with more abundant graminoids, are consistent with expected climate change effects in colder regions of the Arctic. Repeated observations of permanent plots can aid in detecting and understanding long-term ecological change.

Keywords

Climate change; permanent plots; tundra; *Dryas integrifolia*; *Polygonum viviparum*; *Saxifraga oppositifolia*

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Abbreviations

NMDS: non-metric multidimensional scaling
SD: standard deviation

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Introduction

In four decades, the Arctic has exhibited unprecedented, rapid rises in temperature, driven by climate change. The region has warmed almost four times faster than the global average (Rantanen et al. 2022), accompanied by more frequent extremes in temperature and precipitation (Graham et al. 2017; Walsh et al. 2020). Arctic amplification portends serious implications for the biota. Tundra plants, given their key role in ecosystem functioning across trophic levels, represent valuable candidates for monitoring and understanding climate effects (Graae et al. 2009; Myers-Smith et al. 2011; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe et al. 2012; Björkman et al. 2020; Collins et al. 2021).

The anticipated impacts of climate change have spawned an immense effort to document, interpret and

project shifts in the abundance and composition of Arctic vegetation. Although responses may vary, general patterns have emerged. Notably, in the High Arctic where mean summer temperatures do not exceed 10 °C, increases in graminoids are common, whereas in the relatively warmer Low Arctic, shrubs tend to proliferate (Elmendorf, Henry, Hollister, Björk, Björkman et al. 2012; Björkman et al. 2020; Harris et al. 2021; Heijmans et al. 2022). Shrubification may be driven by increased temperatures that extend the growing season and enhance growth (Myers-Smith et al. 2011; Collins et al. 2021). The proliferation of graminaceous and woody plants is often linked to large-scale ‘greening’ of the tundra—increases in plant productivity and cover, typically at warm, high-elevation sites and with rising summer air temperatures and soil moisture. While less common, ‘browning’—the converse of these conditions—has been documented at several

locations, often owing to the die-off of shrubs (Berner et al. 2020).

Nonetheless, discerning changes in Arctic vegetation is a challenge, often clouded by pronounced spatial heterogeneity (Schaefer & Messier 1995b; Ju & Masek 2016), mismatches between short-term and long-term responses (Hill & Henry 2011; Elmendorf, Henry, Hollister, Björk, Bjorkman et al. 2012) and truncated baselines (Mihoub et al. 2017). These are serious impediments to inference. Permanent plots represent a straightforward, yet powerful solution (Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe et al. 2012; Bjorkman et al. 2020; Harris et al. 2021). Indeed, when extended over decades, repeat observations provide both spatial precision and extended duration. Despite their utility, however, long-term, plot-level studies of Arctic flora remain uncommon (Jorgenson et al. 2015; Bjorkman et al. 2020).

Here, I used permanent plots to examine decadal changes in the abundance and composition of vegetation on south-eastern Victoria Island, Arctic Canada. I capitalized on extant data from 80 such plots (Fig. 1) where, in 1991 and 1992, I measured floral abundance and composition as well as soil depth (Schaefer & Messier 1994). To assess changes over the past three decades, I replicated those measurements during 2019 and 2022. Consistent with climate change effects (Bush & Lemmen 2019), I anticipated greening of the tundra, manifesting as an increase in graminoids, typical of comparatively cold regions in the High Arctic

(Kapfer & Grytnes 2017; Myers-Smith et al. 2020), rather than increases in deciduous shrubs, typical of warmer, lower-latitude regions (Myers-Smith et al. 2011; Elmendorf, Henry, Hollister, Björk, Bjorkman et al. 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe et al. 2012; Bjorkman et al. 2020; Harris et al. 2021).

Materials and methods

Study area

My study took place near Wellington Bay, Nunavut, Canada ($69^{\circ}25'15''\text{N}$, $106^{\circ}16'32''\text{W}$). During 1991–93, I quantified vegetation and snow-cover as part of a study of the behaviour and habitat selection of muskoxen (Schaefer & Messier 1994, 1995a, b). The area is classified as non-tussock sedge dwarf-shrub moss tundra of Subzone D: moist tundra, dominated by sedges and dwarf shrubs <40 cm in height (Walker et al. 2005).

Since the late 1940s, temperatures have risen substantially in the nearby community of Cambridge Bay, 60 km to the south-east—by $0.30^{\circ}\text{C}/\text{decade}$ in mean July temperature (Panchen 2016; Buchkowski et al. 2020) and by $0.40^{\circ}\text{C}/\text{decade}$ in mean annual temperature (Buchkowski et al. 2020). Since 1960, winter snow depth has increased by $1.1\text{ cm}/\text{decade}$ (Lam et al. 2022). For the period relevant to my study, I computed from the most recent Environment Canada records (<https://climate.weather>.

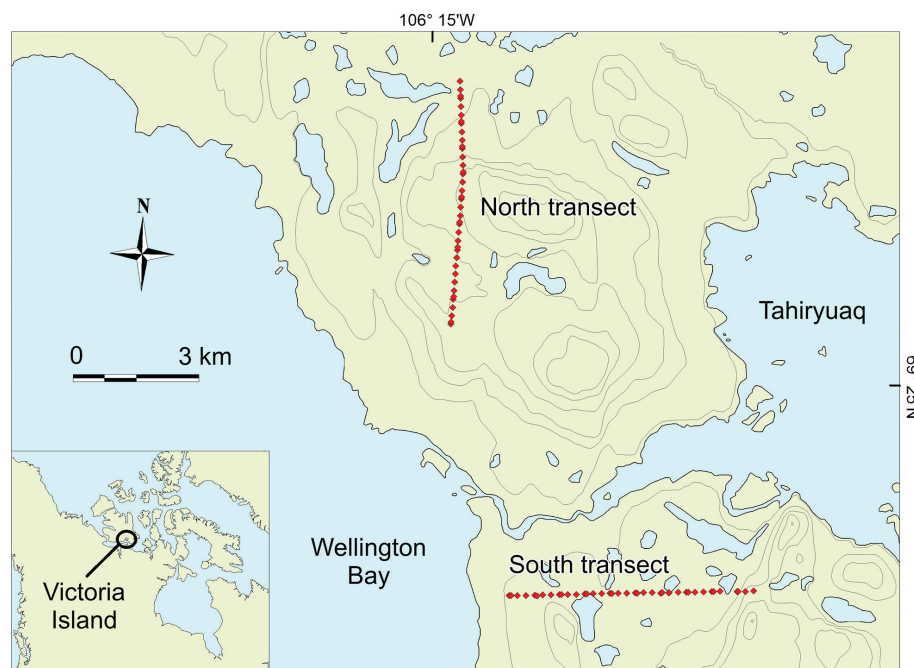


Fig. 1 The study area on south-eastern Victoria Island, Nunavut, Canada, 1991–2022, illustrating the arrangement of permanent plots along two transects. The contour interval is 25 m.

gc.ca) that the average July temperature during 1971–1992 was 7.9 °C, compared to 9.4 °C during 1993–2014. From 1971 to 2014, on average, the mean July temperature rose by 0.49 °C/decade ($p = 0.009$); total July precipitation rose by 4.3 mm/decade ($p = 0.033$).

Data collection and preparation

My observations were derived from plots centred at aluminum stakes, established in 1991. In August of that year, using a topographic map and 100-m tape, my field assistant and I erected the stakes systematically along two transects, each 5.8 km long (Fig. 1). One transect ran south to north, the other west to east. Each transect comprised 30 stakes at 200-m intervals, plus 10 ‘additional’ stakes along the transect, erected 50 m from the first stake and every third stake thereafter. My study comprised 80 stakes in total (Schaefer & Messier 1994).

During 2019 and 2022, I returned to the study area and found all but two of the original stakes. For the two missing stakes, we re-established their locations by interpolating between the pair of neighbouring stakes. We recorded the geographic coordinates of each stake using GPS (Fig. 1).

For this assessment, I compared observations of vegetation and soil from the baseline period, 6–8 and 14 August 1991 and 10–11 and 20 August 1992 (Schaefer & Messier 1994), with those from the contemporary period, 10–13 August 2019 and 13–16 August 2022. I used consistent protocols for these measurements (Schaefer & Messier 1994). We laid a 1 × 1-m plot, centred at each stake and aligned approximately in four cardinal directions and composed of 16 25 × 25-cm contiguous subplots. In each subplot, we estimated the cover of each common species of shrubs, forbs and lichens, as well as the broad categories of graminoids and mosses, in classes of 1%, 5%, 10%, 20%, 30% ... 100%. Hereafter, I refer to all such categories as species, irrespective of taxonomic level. In addition, at each plot, we measured the depth of soil to rock or to permafrost using a metal rod. I also determined elevation, recorded as the lower bound of each 10-m contour interval from 1:50 000 digital topographic maps (CanVec Series, Natural Resources Canada).

I treated the 1-m² plot as the experimental unit. I used two expressions of abundance for each species: cover and frequency (Bonham 2013). For cover, I averaged the values of cover in the 16 subplots. For frequency, I computed the percentage of the 16 subplots that were occupied.

There were some differences in field protocols between periods. During 1991 and 1992, we did not record soil depth in five of the plots. As well, during 1991 and 1992, in the additional plots, we estimated coverage in the whole 1-m² plot (in classes of 1%, 5%, 10%, 20%, 30% ... 100%) rather than in each of 16 subplots. Hence, to make these

vegetation observations comparable between periods, I converted the 2019 and 2022 data in the additional plots to the same format as in 1991 and 1992: I rounded the average cover in the 16 subplots to the nearest cover class (1%, 5%, 10%, 20%, 30% ... 100%) for the whole plot.

These data, plus contemporary photographs of the plots, are available at Borealis, the Canadian Dataverse Repository (dois: 10.5683/SP3/Z9LXDP and 10.5683/SP3/ZRK48T).

Data analyses

To evaluate changes between baseline and contemporary periods, I applied a combination of multivariate and univariate statistics. I retained species with ≥10% frequency, in aggregate for all plots across both periods. I conducted these analyses using Statistica version 13.3 (Tibco), except for the ordination and autocorrelation analyses, for which I used PAST version 4.13 (Hammer et al. 2001).

To characterize the change in each species' abundance across the study area, I calculated the mean cover (and SD) from all 80 plots. To express changes between periods, I computed differences as $c - b$, where c is the mean cover during the contemporary period and b is the mean cover during the baseline period; I also computed the proportional change between periods as $(c - b) / b \times 100\%$. Finally, I calculated the mean frequency (and SD) from all 60 plots (i.e., where subplots were used in both periods).

To test for changes in vegetation abundance, I applied Wilcoxon matched pairs tests (given the lack of normality in paired differences) to the differences in cover and in frequency of each species. Because I considered double-zeros uninformative, I included only cases where the species was present in the plot during at least one of the periods. I omitted plots that were, for example, devoid of soil and vegetation, such as raised beaches ($n = 3$) and lakes ($n = 2$). To control the family-wise error rate, given these multiple tests, I applied a Bonferroni correction (i.e., $\alpha = 0.05 \div 13 \text{ species} \approx 0.004$). I tested the assumption of independence among the plots by computing Moran's I on the differences in graminoid cover (a key study outcome) as a function of the spacing between plot pairs. This correlogram revealed no significant autocorrelation, even at the shortest distance classes (Supplementary Fig. S1). The assumption of independence appears to be satisfied.

In our measurements of soil depth, we could not discern the substrate, whether permafrost or rock. On south-eastern Victoria Island, permafrost is typically 0.5–1.0 m deep (Kim et al. 2021). Therefore, to provide a reasonable approximation of changes in active soil thickness, I focussed on plots where soil was more likely underlain by permafrost rather than rock, i.e., where soil

depth ≥ 50 cm (during 1991 and 1992). I applied Wilcoxon-matched pairs tests to those plots.

To test for correspondence among plot-level changes in vegetation as well as with physical features, I computed Spearman rank correlations to the differences in cover (and in soil depth) among the species displaying significant change between periods: graminoids, *Dryas integrifolia*, *Polygonum viviparum* and *Saxifraga oppositifolia*

(Table 1). To control the family-wise error rate, I applied a Bonferroni correction (i.e., $\alpha = 0.05 \div 10$ correlations = 0.005). I also tested whether these vegetation changes were related to elevation. I computed gamma coefficients (given the numerous ties) between elevation and the changes in cover of these same four species, again with a Bonferroni correction (i.e., $\alpha = 0.05 \div 4$ correlations $\approx$ 0.01). Finally, given the differences in topography

Table 1 Mean cover and frequency of vegetation species, south-eastern Victoria Island, Nunavut, Canada, during the baseline (1991 and 1992) and contemporary periods (2019 and 2022). Significant differences between periods (Bonferroni-corrected $\alpha = 0.004$) are highlighted by *p* values in boldface. Means and SD are based on total number of 1×1 -m plots for cover ($n = 80$) and frequency ($n = 60$).

Species or group	Code	Period	Cover					Frequency				
			Mean (%)	SD	Wilcoxon-matched pairs test			Mean (%) ^a	SD	Wilcoxon-matched pairs test		
					<i>n</i> ^b	<i>Z</i>	<i>p</i>			<i>n</i> ^b	<i>Z</i>	<i>p</i>
Graminoids	GRA	1991, 1992	19.08	15.89	73	2.951	0.0032	91.4	26.6	56	0.943	0.3454
		2019, 2022	22.70	16.73				92.6	25.2			
<i>Dryas integrifolia</i>	DRY	1991, 1992	17.97	12.73	69	5.574	<0.0001	76.3	37.0	53	0.943	0.3458
		2019, 2022	11.51	9.84				74.4	36.4			
<i>Salix</i> spp.	SSP	1991, 1992	4.12	5.01	61	1.411	0.1582	42.7	35.0	46	1.038	0.2994
		2019, 2022	3.56	4.81				39.4	34.7			
<i>Salix richardsonii</i>	SAR	1991, 1992	2.77	5.99	38	0.120	0.9047	14.2	26.8	29	1.171	0.2416
		2019, 2022	2.55	4.94				16.3	27.8			
<i>Equisetum</i> spp.	EQU	1991, 1992	0.10	0.27	21	0.568	0.5700	7.0	20.3	15	0.471	0.6378
		2019, 2022	0.13	0.30				6.7	19.1			
<i>Pedicularis</i> spp.	PED	1991, 1992	0.46	0.83	60	0.849	0.3958	14.4	16.4	50	1.000	0.3173
		2019, 2022	0.38	0.64				11.7	16.7			
<i>Oxytropis</i> spp.	OXY	1991, 1992	0.86	2.00	32	2.019	0.0434	13.3	23.3	27	0.925	0.3550
		2019, 2022	0.46	0.99				10.9	19.5			
<i>Polygonum viviparum</i>	POL	1991, 1992	0.35	0.39	53	3.752	0.0002	25.5	27.1	40	4.591	<0.0001
		2019, 2022	0.20	0.34				9.5	17.4			
<i>Saxifraga oppositifolia</i>	SAX	1991, 1992	0.97	1.68	40	5.090	<0.0001	21.9	28.9	31	4.552	<0.0001
		2019, 2022	0.10	0.25				4.6	9.8			
<i>Cassiope tetragona</i>	CAS	1991, 1992	0.94	2.81	15	2.229	0.0258	9.0	26.1	9	0.770	0.4412
		2019, 2022	0.36	1.06				7.2	23.7			
Mosses	MOS	1991, 1992	4.06	5.34	74	2.575	0.0100	56.6	36.1	56	2.364	0.0181
		2019, 2022	2.90	3.88				45.3	34.7			
<i>Cetraria cucullata</i>	CEC	1991, 1992	0.98	2.00	39	0.231	0.8175	26.4	36.4	30	2.179	0.0293
		2019, 2022	0.95	1.88				20.9	33.2			
<i>Cetraria nivalis</i>	CEN	1991, 1992	0.15	0.43	20	0.189	0.8498	8.1	24.1	14	0.245	0.8068
		2019, 2022	0.18	0.45				9.0	24.1			

^aFrequency expressed as percent occupancy in 25×25 -cm subplots. ^bFor the Wilcoxon tests, *n* = number of paired 1×1 -m plots where the species was present during at least one period.

between North and South transects, I tested for differences between transects in the changes in cover of these four species using Mann–Whitney tests.

To characterize shifts in vegetation communities, I carried out NMDS based on a matrix of euclidean distances (Kenkel & Orloci 1986) using the vegetation data from both periods. I tested for changes between periods with Wilcoxon-matched pairs tests on scores on each of the first two NMDS axes. To depict relationships of flora with the physical environment, I included soil depth and elevation as supplementary variables in the ordination. To test for relationships between these physical features and vegetation, as well as their consistency between periods, I computed Spearman correlations (for soil) and gamma (for elevation) to score on the first two NMDS axes, separately for each axis and each period. Again, to maintain a conservative family-wise error rate, I applied a Bonferroni correction (i.e., $\alpha = 0.05 \div 8$ correlations ≈ 0.005).

Results

After three decades, the permanent plots at Wellington Bay displayed appreciable shifts in vegetation abundance and composition (Table 1, Fig. 2). Compared to the baseline period, the contemporary period showed an increase in graminoids (proportional change in cover = +19%) and declines in *Dryas integrifolia* (−36%), *Polygonum viviparum* (−43%) and *Saxifraga oppositifolia* (−90%; Fig. 2). The decline in *Dryas integrifolia*, in particular, was noticeable as patchy, apparent mortality of this shrub, in the plots and elsewhere (Fig. 3). I detected no significant changes in other forbs and shrubs, nor in lichens, although declines in the cover of *Cassiope tetragona* ($p = 0.026$) and in the cover ($p = 0.010$) and frequency ($p = 0.018$) of mosses were marginally statistically significant (Bonferroni-corrected $\alpha = 0.004$; Table 1). Only species with the largest declines in cover showed significant

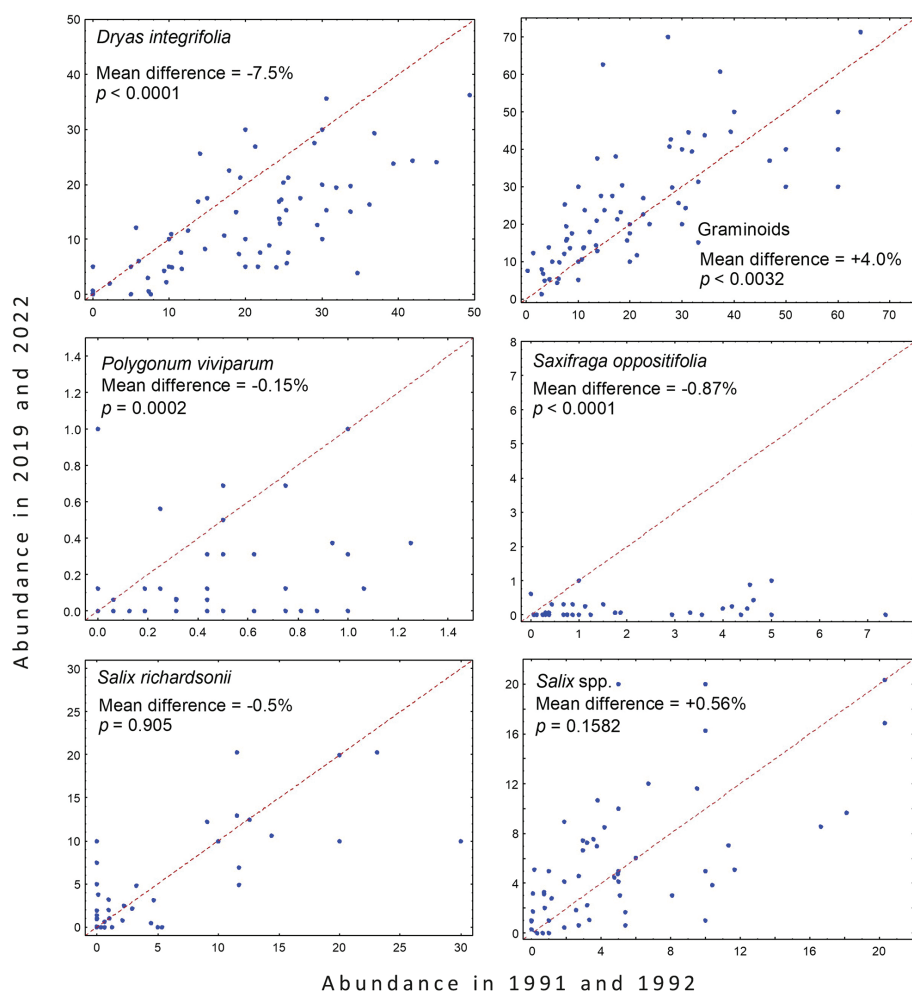


Fig. 2 Cover of plant species between baseline (1991 and 1992) and contemporary (2019 and 2022) periods in the study area. The dashed line ($Y = X$) represents equality between periods. Results of the Wilcoxon-matched pairs test are shown in each panel.

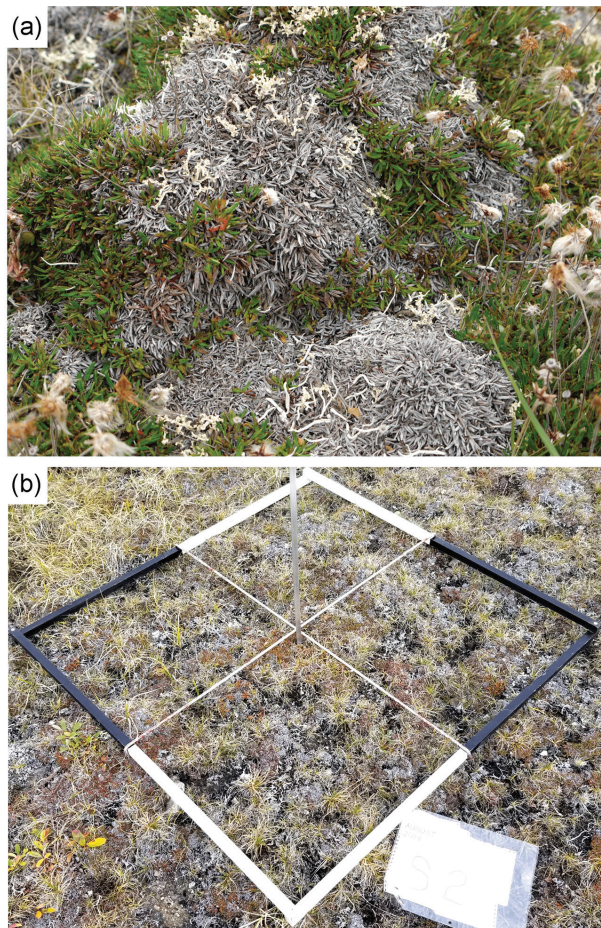


Fig. 3 (a) An example of apparent dieback of *Dryas integrifolia*, photographed in August 2022. (b) A 1 × 1-m plot, photographed August 2019, in which the abundance of *D. integrifolia* declined by more than half compared to the baseline period—from 29.4% cover in 1991 to 12.6% cover in 2019.

changes in frequency: *Polygonum viviparum* (25.5 to 9.5%) and *Saxifraga oppositifolia* (21.9 to 4.6%). Soil was significantly deeper during the contemporary period when analysed across all plots (mean = +7.9 cm; $n = 70$, $Z = 3.582$, $p < 0.001$), but I found no significant change in the plots more likely underlain by permafrost, i.e., with ≥ 50 cm soil depth ($n = 26$, $Z = 0.161$, $p = 0.872$). Even within a plot, soil depth was often erratic.

I found little correspondence among these changes among species. Based on Spearman rank correlations, difference in soil depth was not significantly correlated with differences in the cover of graminoids, *Dryas integrifolia*, *Polygonum viviparum* and *Saxifraga oppositifolia* ($-0.108 < r_s < 0.075$; $p > 0.05$). Nor were the differences in cover among these four species significantly correlated with each other ($-0.383 < r_s < 0.122$; $p > 0.01$; Bonferroni-corrected $\alpha = 0.005$). On the other hand, based on the

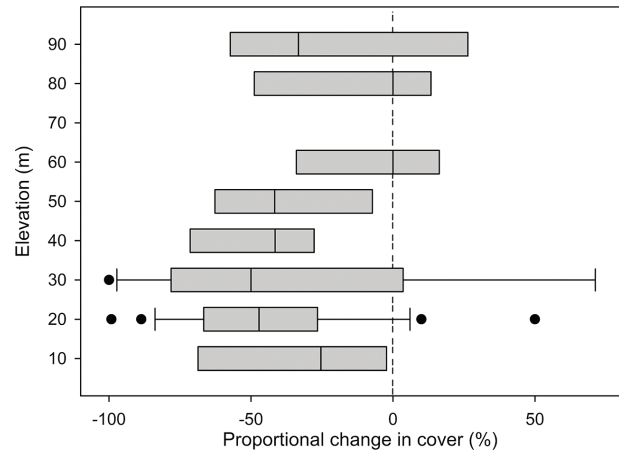


Fig. 4 Proportional change in the cover of *Dryas integrifolia* in the study area, between baseline (1991 and 1992) and contemporary periods (2019 and 2022) relative to elevation. Elevation classes are expressed as the lower bound of each contour interval. Boxes denote 25th and 75th percentiles; lines inside the boxes indicate medians; whiskers indicate 90th and 10th percentiles; and points indicate outliers.

gamma coefficient, differences in the cover of *Dryas integrifolia* were noticeably related to topography, with larger declines at lower elevations ($\gamma = 0.267$, $n = 69$, $Z = 2.939$, $p = 0.003$; Fig. 4). Similarly, given that the North transect traversed generally higher elevations (Fig. 1), the decline in *D. integrifolia* was more pronounced along the South transect (Mann–Whitney test; $p = 0.043$; Supplementary Table S1). Changes in the other three species were neither significantly related to elevation ($p > 0.15$) nor appreciably different between the two transects ($p > 0.064$), although *Saxifraga oppositifolia* showed marginally larger declines at higher elevations ($\gamma = -0.250$, $n = 40$, $Z = 2.100$, $p = 0.034$; Bonferroni-corrected $\alpha = 0.01$).

Despite the lack of correspondence in changes among species pairs, NMDS revealed a community shift toward more abundant graminoids coupled with reductions in several shrubs and forbs (Fig. 5). Compared to the baseline period, scores during the contemporary period were significantly lower on the first ($n = 80$, $Z = 3.616$, $p < 0.001$) and second axes ($n = 80$, $Z = 4.720$, $p < 0.001$; Bonferroni-corrected $\alpha = 0.005$), reflecting the gain in graminoids and the losses in such species as *Cassiope tetragona*, *Dryas integrifolia*, *Oxytropis* spp., *Polygonum viviparum* and *Saxifraga oppositifolia* (Fig 5). Moreover, soil depth was correlated with the vegetation assemblages, as revealed by its negative correlations with scores on the first axis during the baseline ($r_s = -0.422$, $n = 74$, $p < 0.001$) and contemporary periods ($r_s = -0.479$, $n = 79$, $p < 0.001$), but not with scores on the second axis during either period ($r_s < 0.275$, $p > 0.017$; Bonferroni-corrected $\alpha = 0.005$). Elevation, too, was positively correlated with the scores on first NMDS

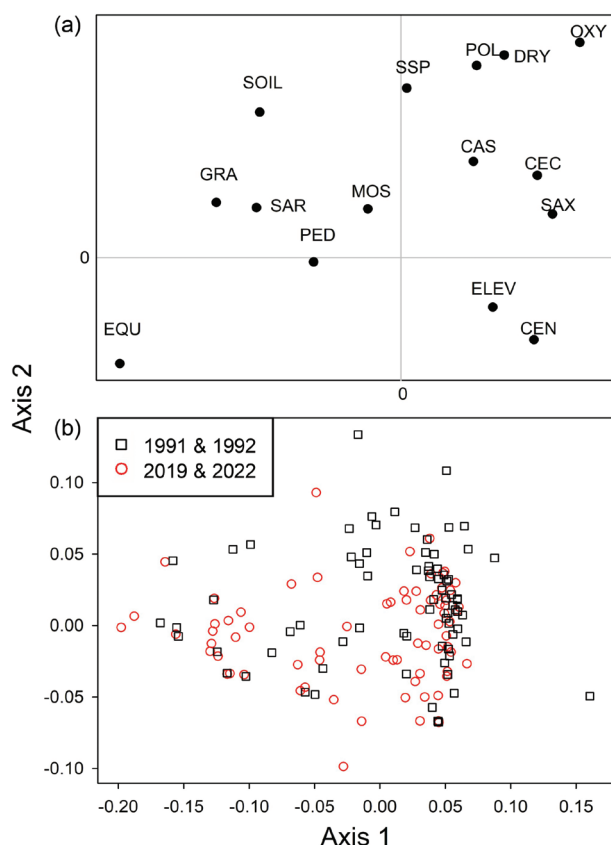


Fig. 5 NMDS of vegetation during baseline (1991 and 1992) and contemporary (2019 and 2022) periods. (a) Column scores of species; elevation (ELEV) and soil depth (SOIL) are included as supplementary variables (at 1:10 scale). Species codes as in Table 1. (b) Scores on the first two NMDS axes for plots during the baseline (1991 and 1992) and contemporary (2019 and 2022) periods.

axis during the contemporary period ($\gamma = 0.236$, $n = 80$, $p = 0.005$), a pattern that was only marginally significant during the baseline period ($\gamma = 0.211$, $n = 80$, $p = 0.011$). Scores on the second axis were not correlated with elevation during either period ($-0.172 < \gamma < 0.008$, $p > 0.039$; Bonferroni-corrected $\alpha = 0.005$). Largely irrespective of period, graminoid-dominated communities were characterized by deeper soils and lower elevations (Fig. 5).

Discussion

On south-eastern Victoria Island, a region undergoing rapid climate change (Panchen 2016; Bush & Lemmen 2019; Buchkowski et al. 2020), I discovered pronounced shifts in vegetation after three decades: a marked increase in graminoids, along with substantial declines in *Dryas integrifolia*, *Polygonum viviparum* and *Saxifraga oppositifolia* (Table 1, Figs. 2, 5). Without repeated observations, these

changes likely would have gone undetected. For example, when plots were treated as pairs, the rise in graminoid cover was evident in 63% of cases (i.e., 46/73 observations above the line of equality; Fig. 2), but this increase was statistically insignificant when the data were treated as independent samples (Mann–Whitney U test, $n_1 = n_2 = 80$, $p = 0.130$). The value of permanent plots is clear. Indeed, parsing out spatial variation and discerning temporal change in the Arctic may depend on longitudinal studies that span decades (Elmendorf, Henry, Hollister, Björk, Bjorkman et al. 2012; Panchen & Gorelick 2015; Panchen et al. 2021).

Nevertheless, despite the wealth of evidence of climate effects on Arctic flora (Elmendorf, Henry, Hollister, Björk, Bjorkman et al. 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe et al. 2012; Collins et al. 2021), observational studies such as mine may be prone to other, confounding influences. Here, two factors deserve consideration. First, caribou and muskoxen, important herbivores in the region, were numerous during the 1990s to mid-2000s; both species are likely food-limited (Schaefer & Messier 1995a; Tomaselli et al. 2018). However, caribou were transient in the study area; muskoxen displayed only modest grazing and browsing intensity (Schaefer & Messier 1995a), implying negligible effects of large herbivore foraging. Second, these permanent plots were also monitored for nival conditions during two winters, when we cut vertical snow profiles close to the stake and potentially disturbed the vegetation (Schaefer & Messier 1995b). I cannot entirely discount that this activity may have caused at least some of the vegetation change. My inferences should, therefore, be treated cautiously.

General patterns are emerging of how Arctic vegetation responds to climate change. These syntheses reveal, for instance, that warming often induces greening of the tundra, typically driven by the proliferation of shrubs at lower latitudes and graminoids at higher latitudes (Elmendorf, Henry, Hollister, Björk, Bjorkman et al. 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe et al. 2012; Bjorkman et al. 2020; Heijmans et al. 2022). At the same time, browning of the tundra, potentially serious declines in biomass and productivity, is not uncommon (Berner et al. 2020; Myers-Smith et al. 2020). Many responses are also site- and species-specific (Bjorkman et al. 2020), underscoring that ecology is rife with interactions.

My results largely align with these expectations. Most notably, the increase in graminoids was widespread and substantial—in three decades, a proportional change in cover of +19% (Table 1; Fig. 2). Graminoids often respond positively to warming (Kapfer & Grytnes 2017; Bjorkman et al. 2020) and perhaps more rapidly to weather conditions than other plant groups (Jorgenson et al. 2015).

Increases in graminoids tend to prevail at colder Arctic sites (summer temperature <10 °C; Hill & Henry 2011; Elmendorf, Henry, Hollister, Björk, Bjorkman et al. 2012), such as Wellington Bay. As dominant plants (Schaefer & Messier 1994), such shifts in graminaceous vegetation likely constitute important changes at the ecosystem level (Hill & Henry 2011). Sedges and grasses are principal forages for muskoxen and caribou (Schaefer and Messier 1995a; COSEWIC 2017), and they differ markedly from other plant growth forms in their effects on nutrient cycling (Hobbie 1996).

The greening of the tundra is not universal, however (Berner et al. 2020). In my study, the decline in *Dryas integrifolia*—whose abundance fell by more than one-third (Fig. 2)—contributed to patchy browning at many locales (Fig. 3). This dwarf shrub is sensitive to temperature variations (Robinson & Henry 2018; Panchen 2022) and may exhibit recruitment failure in the face of temperature extremes (Panchen et al. 2021). The decline of *D. integrifolia* was more precipitous at lower elevations (Fig. 4) reflecting wetter conditions (Schaefer & Messier 1994), consistent with greater community responses in moist habitats (Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe et al. 2012; Bjorkman et al. 2020) and browning at low elevation (Berner et al. 2020). Rain-on-snow events, likely to increase in the Arctic (Walsh et al. 2020), can contribute to such browning (Phoenix & Bjerke 2016; Bjerke et al. 2017).

Although diminutive in stature, *Polygonum viviparum* and *Saxifraga oppositifolia* also displayed sharp reductions in both cover and frequency (Table 1), including their disappearance from several plots (Fig. 2). For *Polygonum viviparum*, responses to climate change have been variable. Under experimental conditions, this forb exhibited lower establishment after warming (Graae et al. 2009) and reduced physiological performance after successive heatwaves (Marchand et al. 2006). In observational studies, however, *P. viviparum* increased at some High Arctic sites over decades (Hill & Henry 2011; Kapfer & Grytnes 2017), whereas the species disappeared from an alpine site in Vermont over the course of a century (Zika 1993). *Saxifraga oppositifolia* appears susceptible to warming, drought stress and competition from other plants (Panchen & Gorelick 2015; Kobiv 2017; Opala-Owczarek et al. 2018), evident as lower growth and impaired reproductive performance (Stenström et al. 1997). While I am unaware of declines of *S. oppositifolia* elsewhere, Panchen & Gorelick (2015) reported the disappearance of five of 25 plants during seven years of monitoring, implying an appreciate rate of mortality. At Wellington Bay, corroboration of the decreasing trends in *Polygonum viviparum*, *Saxifraga oppositifolia* as well as the marginal declines in mosses and *Cassiope tetragona*

(Table 1)—from local knowledge or extensive plant surveys, for instance—would be valuable.

Lack of change constitutes the most frequent response of Arctic vegetation to warming (Pattison et al. 2015; Bjorkman et al. 2020), including most species in my study (Table 1). I also failed to detect a change in soil depth (Hill & Henry 2011), a feature prone to year-to-year variation and inconsistent short-term trends (Smith et al. 2017). For the flora, the absence of change also implies some climatic resistance, at least over decades (Prach et al. 2010; Bjorkman et al. 2020; Jónsdóttir et al. 2023). The lack of shrubification—there were discernable increases neither in the erect willow *Salix richardsonii* nor in prostrate willows (Fig. 2)—reiterates patterns elsewhere in the High Arctic (Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe et al. 2012; Kapfer & Grytnes 2017; cf. Hill & Henry 2011), as well as at Walker Bay, 140 km to the south-west (Buchkowski et al. 2020). Declines in mosses—in my study, manifest in both cover and frequency, albeit marginally significant (Table 1)—is another widespread trend (Elmendorf, Henry, Hollister, Björk, Bjorkman et al. 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe et al. 2012; Bjorkman et al. 2020).

Conclusion

For deciphering vegetation change, my study highlights the leverage from repeated, spatially precise observations. At the same time, such mensurative studies may be prone to confounding influences (Collins et al. 2021), underscoring the need for corroboration and for caution in interpretation. After three decades at the Wellington Bay, the changes in vegetation—in particular, more abundant graminoids but no apparent change in willows—are consistent with shifts in relatively cold regions of the High Arctic. With continuing warming, where summer temperatures could soon exceed 10 °C, a transition to shrub expansion might be anticipated (Elmendorf, Henry, Hollister, Björk, Bjorkman et al. 2012). Sustained monitoring will be key to testing that hypothesis.

In ecology, understanding long-term change demands long-term investment (Lindenmayer et al. 2015). At the same time, the rapidity of Arctic climate change (Bush & Lemmen 2019; Rantanen et al. 2022) underscores the urgency to assembling key knowledge about the biota. Retrospective analyses from permanent plots can provide immediate opportunities to uncover long-term trends. Seizing opportunities for sustained monitoring, for example, using permanent plots and taking advantage of existing data sets, will be an important part of that effort.

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