ARTICLE

Understanding the climate impacts on decadal vegetation change in northern Alaska[1]

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Abstract: The Arctic is experiencing rapid climate change. This research documents changes to tundra vegetation near Atqasuk and Utqiaġvik, Alaska. At each location, 30 plots were sampled annually from 2010 to 2019 using a point frame. For every encounter, we recorded the height and classified it into eight groupings (deciduous shrubs, evergreen shrubs, forbs, graminoids, bryophytes, lichens, litter, and standing dead vegetation); for vascular plants we also identified the species. We found an increase in plant stature and cover over time, consistent with regional warming. Graminoid cover and height increased at both sites, with a 5-fold increase in cover in Atqasuk. At Atqasuk, the cover and height of shrubs and forbs increased. Species diversity decreased at both the sites. Year was generally the strongest predictor of vegetation change, suggesting a cumulative change over time; however, soil moisture and soil temperature were also predictors of vegetation change. We anticipate that plants in the region will continue to grow taller as the region warms, resulting in greater plant cover, especially of graminoids and shrubs. The increase in plant cover and accumulation of litter may negatively impact non-vascular plants. Continued changes in community structure will impact energy balance and carbon cycling and may have regional and global consequences.

Key words: tundra, vegetation change, plant height, climate change, ITEX.

Résumé : L'Arctique connaît un changement climatique rapide. Cette recherche documente les changements de la végétation de la toundra près d'Atqasuk et d'Utqiaġvik, en Alaska. À chaque emplacement, 30 parcelles ont été échantillonnées chaque année de 2010 à 2019 en utilisant un cadre de criblage systématique. Pour chaque rencontre, les auteurs ont enregistré la hauteur et l'ont classée en huit groupes (arbustes à feuilles caduques, arbustes à feuilles persistantes, herbes non graminéennes, graminoïdes, bryophytes, lichens, litière et végétation morte sur pied) ; pour les plantes vasculaires, ils ont aussi identifié l'espèce. Ils ont constaté une augmentation de la hauteur et du couvert des végétaux au fil du temps,

ce qui correspond au réchauffement régional. Le couvert et la hauteur des graminées augmentaient sur les deux sites, avec un couvert cinq fois plus important à Atqasuk. À Atqasuk, le couvert et la hauteur des arbustes et des herbes augmentaient. La diversité des espèces diminuait sur les deux sites. L'année était généralement le prédicteur le plus fort du changement de végétation, ce qui suggère un changement cumulatif au fil du temps ; toutefois, l'humidité et la température du sol étaient également des prédicteurs du changement de végétation. Les auteurs prévoient que les plantes de la région continueront de croître en hauteur à mesure du réchauffement de la région, ce qui entraînera un plus grand couvert végétal, en particulier des graminoïdes et des arbustes. L'augmentation du couvert végétal et l'accumulation de la litière peuvent avoir un impact négatif sur les plantes non vasculaires. Les changements continus de la structure de la communauté auront un impact sur le bilan énergétique et le cycle du carbone et pourraient avoir des conséquences régionales et mondiales. [Traduit par la Rédaction]

Mots-clés : toundra, changement de végétation, hauteur des plantes, changement climatique, ITEX.

Introduction

Anthropogenic climate change has been documented for over a century, although the intensity of change has increased over the past few decades, global temperatures may increase by as much as approximately 5 °C over the next 100 years (IPCC 2018). High-latitude regions may expect at least twice the rate of warming in lower-latitude regions (AMAP 2019). The observed warming trend is of interest because the Arctic region is particularly sensitive to climate change and, in part, responsible for balancing the global atmospheric carbon budget and regulating the energy balance of the Earth (Chapin et al. 2000). Vegetation responses to climate change are a focal point of research because vegetative communities are determined, at least partially, by regional climate. Generally, Arctic plants are limited by the cold conditions in which they are found (cold and freezing temperatures, low nutrient availability) (Chapin 1983; Chapin et al. 1995). Therefore, plants tend to respond to warming with enhanced growth and life cycle progression (Arft et al. 1999; Hollister and Flaherty 2010) and increased reproductive success (Myers-Smith et al. 2011), although there is evidence that this effect may wane with time (Kremers et al. 2015). An extension of the growing season, warmed air temperatures, and hastened rate of snowmelt are largely responsible for this enhanced growth and life cycle progression (Walther 2010; Oberbauer et al. 2013). Warming of the Arctic may cause increased rates of soil organic matter decomposition and enhanced greenhouse gas emissions, leading to an increase and acceleration of warming. The positive feedback loop of increasing greenhouse gas emissions has global consequences (Rustad et al. 2001; Melillo et al. 2002; Davidson and Janssens 2006). The permafrost regions of the Northern Hemisphere hold approximately twice as much carbon as is currently present in the atmosphere (Zimov et al. 2006; Tarnocai et al. 2009). It is likely that 5% to 15% of this carbon is vulnerable to decomposition and entering the atmosphere within this century (Schuur et al. 2015).

It is difficult to forecast the vegetation response to warming because changes in environmental conditions, in addition to air temperature, may significantly alter the Arctic vegetation. Soil moisture is a major controlling factor of the species composition for any given geographic area; this is equally true in tundra vegetation (Chapin et al. 1996; Phoenix et al. 2001; Gamon et al. 2013). Soil moisture and soil temperature are limiting factors for the decomposition rates of plant litter (Hobbie 1996; Shaver et al. 2006), which subsequently affects carbon and nitrogen cycling within a community. Increases in labile phosphorous via soil organic matter decomposition have been shown to increase soil respiration rates with increases in soil nitrogen (Liu et al. 2021). Soil temperature, which can vary

significantly from air temperature, is a known influencer of plant phenological progression (Oberbauer et al. 1998), overall nutrient availability (Melillo et al. 2002), and net primary productivity (Natali et al. 2012). The growing season soil thaw depth is another important abiotic factor affecting plant communities, as it directly impacts soil moisture and nutrient availability, which in turn influences community growth rates and composition (Anisimov and Reneva 2006; Schuur et al. 2007).

Plants are a critical component of terrestrial ecosystems. As net primary producers, they provide bottom-up control for other trophic levels of the entire ecosystem. Thus, the characteristics of a plant community influence herbivory patterns via variations in forage quality or quantity (Augustine and McNaughton 1998; Joly et al. 2009) and energetic exchanges within ecosystems (Post and Forchhammer 2008), which ultimately affect animal community composition (Orians and Wittenberger 1991; Rettie and Messier 2000). Additionally, plant species differ in their impacts on nutrient cycling, resource partitioning, and ultimately soil nutrient dynamics, which have ecosystem-wide implications (Vinton and Burke 1995).

Long-term studies of Arctic plant communities and their responses to environmental variability are needed to document and better understand the drivers of tundra vegetation change, in light of extended growing seasons, prolonged exposure to summer temperatures, and fluctuations in soil moisture and soil thaw depth (Blok et al. 2011). For example, significant increases in plant cover have been attributed to regional warming at many locations across the Arctic (Hudson and Henry 2009; Jorgenson et al. 2015; Myers-Smith et al. 2019). Documented changes also include advances in tree lines (Harsch et al. 2009; Myers-Smith and Hik 2018) and shrubification of existing tundra (Forbes et al. 2010; Hallinger et al. 2010; Elmendorf et al. 2012; Grigoriev et al. 2020). Detailed information on plant cover and height provides the building blocks necessary for understanding the changes in the competitive interactions between species and functional groups, and enable better prediction of changes in canopy structure and its implications on energy balance and habitat for migratory birds or yearlong resident mammals, and arthropods (Post and Forchhammer 2008; Gilg et al. 2009; Gauthier et al. 2013; Asmus et al. 2018).

This study examines a decade of vegetation change at two locations in the northernmost Alaska in relation to regional warming and other environmental factors. The findings will be of value to researchers working in both low and coastal Arctic environments. The following specific questions were addressed:

1. How have plant cover, height, and diversity changed over time?
2. What are the drivers of vegetation change?
3. Are the drivers of vegetation change consistent across locations?

Materials and methods

Study sites

Two study sites in northern Alaska were sampled: one near the Arctic Ocean coast at Utqiaġvik (formerly Barrow), Alaska (71°19′N, 156°36′W), and the other approximately 100 km south of Atqasuk, Alaska (70°27′N, 157°24′W) (Fig. 1). Utqiaġvik was defined as Biozone C and Atqasuk as Biozone D by Raynolds et al. (2006). Utqiaġvik and Atqasuk are both in region W1 (sedge/grass, moss wetland) on the circumpolar vegetation map (CAVM Team 2003). At each location, long-term 1 m² plots were laid out in a 1 km² grid with approximately 100 plots spaced 100 m apart, which was originally established to monitor long-term terrestrial ecosystem change by the Arctic System Science Program, and is sometimes referred to as the ARCSS grid, which is how they will be referenced in this manuscript. The grids are also used by the Circum-Arctic Active Layer Monitoring

Fig. 1. Locations of Atqasuk (red) and Utqiaġvik (blue) on the North Slope of Alaska (Google Earth 2020).
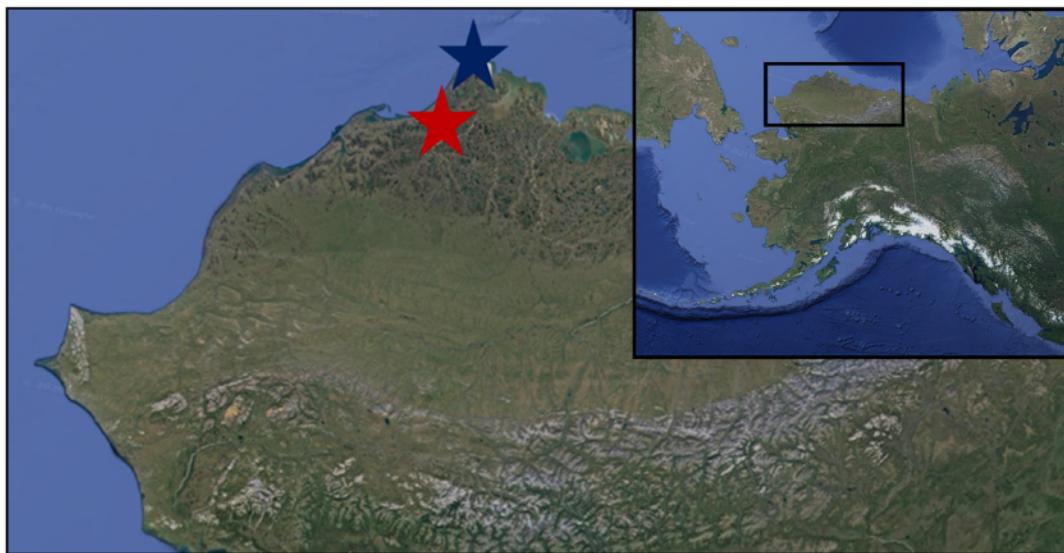
Program and are often referred to as CALM grids (Hinkel and Nelson 2003). Both grids have a subset of 30 plots that are sampled annually, which is the focus of this study. Habitats within the Atqasuk grid include dry, raised ridges, moist tussock tundra, saturated meadows and ponds, and ice-wedge polygons. Habitats within the Utqiaġvik grid range from dry, raised ridges to saturated meadows and ponds, and also include ice-wedge polygons. A small amount of vehicle disturbance occurs from winter snow machines and the rare but more impactful occurrence of summer ATV traffic. No vehicles directly impacted any plots during the sampling period; however, there was minor foot disturbance near the plots due to repeated sampling, which was more pronounced in the water-saturated areas. The plots described here are adjacent to, but not part of, the warming experiments at the International Tundra Experiment (ITEX) sites (Hollister et al. 2006; Hollister et al. 2015).

Climate monitoring

Weather stations were installed within the ARCSS grids at both Atqasuk and Utqiaġvik in the 1990s as part of the International Tundra Experiment sites. Air temperature (°C) was measured at a height of 2 m from the ground using a model 107 temperature probe (Campbell Scientific Inc., Logan, Utah, USA). Precipitation (cm) was measured with a 35-cm TE525 tipping bucket rain gauge (Campbell Scientific Inc.). These data were logged every hour using a CR10X datalogger (Campbell Scientific Inc.). Further details regarding climate monitoring at these sites are available in Hollister et al. (2006). Thawing degree day values (the average of temperatures above 0 °C, summed daily) were calculated from the temperature measurements obtained from either weather station. Plot level environmental variables, collected every 1–2 weeks throughout each summer, included soil moisture as unitless volumetric water content measured with a FieldScout TDR 300, which records soil moisture as a single value at a depth of 10 cm, soil temperature (°C) obtained by a Weber 6492 thermometer at a depth of 10 cm, and soil thaw depth (cm) with a graduated steel probe. All values used in this analysis were collected between June 15 and July 15 to examine the relationship between vegetation and abiotic factors occurring during the

sampling field season. Measurements were typically taken in the afternoon. Soil temperatures were not collected at Utqiaġvik in 2010 and Atqasuk in 2015, and soil thaw depth was not collected at Atqasuk in 2013.

Vegetation sampling

Plots were sampled annually from 2010 to 2019, excluding 2011. The method used for vegetation sampling was a nondestructive point frame, as described in the ITEX manual (Molau and Mølgarrd 1996). Point framing occurred from early July to mid-August. Each individual plot was sampled within a 14 day-of-the-year range across years to minimize differences in phenological progression between years. A 75 cm^2 100-point frame with point coordinates spaced 7.5 cm apart was raised on aluminum rods to just above the observed canopy height. Each plot had permanent markers affixed to the ground that were used to align the frame to attempt to measure the exact same points at each yearly sampling. Each point was measured with a graduated rod to assess plant identity, living status, and position in the canopy. All of the plants contacted by the rod were counted as occupying that coordinate, with no set maximum number of occupants per coordinate point, which is a modification of the method described by Walker (1996) because it included all encounters (May and Hollister 2012). Vascular plants were identified to species and assigned to functional groups. Nonvascular plant encounters were grouped by functional group. The following functional groups were used in this analysis: deciduous shrub; evergreen shrub; forbs; graminoids; bryophytes; lichens; leaf litter; and standing dead vegetation. Nonvascular plants were grouped as follows: acrocarpous mosses; pleurocarpous mosses; crustose lichens; foliolose lichens; and fruticose lichens.

Cover was calculated as the sum of all encounters in a plot. Species height (cm) was calculated as the height of the encounter relative to the ground. For the height analysis, we used the maximum height of each taxon (functional group or species) per plot.

Data analysis

All statistical analyses were performed using R software for statistical computing v. 3.6.2 (R Core Team 2019). When calculating cover for each plot, all 30 plots were used regardless of whether a functional group or species was encountered in the plot for a given year (i.e., zeros were entered into the resulting database). Species visibly present in a plot but not encountered during point-framing were given a value of 0.1 for the year in which they were present. When calculating height metrics, only plots in which a functional group or species occurred for all nine sampling years were included in the analysis; thus, a variable number of plots were used for each functional group or species (i.e., the sample size varied between taxa based on frequency). Nonvascular plants were omitted from height analysis. Only taxa that had over 200 encounters throughout all sampling years were included in the cover and height analyses. For a complete list of species represented by functional groups (see the Supplementary data, File S1, Table S1[2]). To calculate diversity metrics, only vascular species that occurred in five or more plots for a single year were used, to minimize inconsistencies in the sampling of very rare species. "Alpha diversity" was calculated as the total number of vascular plant species that occurred in a given plot. "Gamma diversity" was calculated as the total number of vascular plant species that occurred throughout the site (all 30 plots) in a given year. "Beta diversity" was calculated by dividing gamma diversity by alpha diversity. Shannon's index and Pielou's evenness diversity indices were calculated using the R package "vegan" (Oksanen et al. 2019).

The distribution of datasets was checked using the Shapiro–Wilk normality test. If a dataset did not approximate a normal distribution after data transformation attempts, then nonparametric tests were used. For cover analyses, a Bayesian Poisson regression was used to model the relationship between plant cover and abiotic factors, including time, and to model the relationships between the cover of functional groups used while accounting for the non-normality of the dataset due to the presence of many zeros. The packages "rstan" (Stan Development Team 2020) and "brms" (Bürkner 2018) were used to enable the Bayesian analyses. A Poisson distribution was assumed because of the count-based nature of the dataset. Bayesian regression models were considered significant if the credible intervals for the model did not overlap zero. For Bayesian regression, we chose the widely applicable information criterion (WAIC) as a means of comparing models that share the same regressed variable. For height analyses, a general linear mixed model was used to model the relationships between the height of functional groups and abiotic variables using the package "lme4" (Bates et al. 2015). Marginal r^2 was obtained from a function within the package "MuMIn" (Barton 2019). Diversity indices were also modeled using linear mixed models. Abiotic trends over time were measured using Spearman's rho test.

Results

Abiotic factors

At Atqasuk, all of the abiotic factors we measured were positively correlated with year (Supplementary data, File S1, Tables S1 and S2[2]). At Utqiaġvik, the abiotic factors positively correlated with year were average air temperature, maximum air temperature, thawing degree day sums, maximum soil temperature, sum of precipitation, and average soil moisture (Fig. 2; Supplementary data, File S1, Tables S1 and S2[2]). The data used may be found in the Supplementary data (File S2[2]).

Vegetation cover

At Atqasuk, the cover of all vascular plant functional groups increased over time (years): deciduous shrubs, from 11.5% to 26.1%; evergreen shrubs, from 12.2% to 29.6%; forbs, from 3.2% to 6.4%; and graminoids, from 20.7% to 108.4%. The cover of litter also increased, from 27.7% to 67.2% (Fig. 3; Supplementary data, File S1, Table S1[2]). There was an increase in the cover of the following vascular plant species: *Betula nana*, *Salix pulchra*, *Vaccinium vitis-idaea*, *Rubus chamaemorus*, *Carex aquatilis*, *Carex. bigelowii*, *Eriophorum angustifolium*, *Eriophorum russeolum*, and *Eriophorum vaginatum*. There was a decrease in cover for only two species: *Pedicularis lapponica* and *Luzula confusa*. In Utqiaġvik, graminoids increased in cover from 43.1% to 104.7% (Fig. 3; Supplementary data, File S1, Table S1[2]). The only vascular plant species to increase in cover were *E. russeolum* and *E. triste*, whereas the following species showed a decline in cover: *Cerastium beeringianum*, *Stellaria humifusa*, *Alopecurus magellanicus*, and *Luzula arctica*. Acrocarpous mosses have also declined in abundance in recent years. The goodness of fit between the cover of associated functional groups is provided for each location in the Supplementary data (File S1, Table S3[2]). The data used may be also be found in the Supplementary data (File S3[2]).

Vascular plant diversity

At both Atqasuk and Utqiaġvik, the values for alpha, beta, and gamma diversity did not vary significantly between years (Table 1). However, the values for Shannon's index at Utqiaġvik (1.4 to 1.3, $r^2 = 0.02$) and Pielou's evenness (0.8 to 0.7, $r^2 = 0.04$) at Atqasuk varied significantly by year and declined over time. In Atqasuk, the values for gamma diversity were 26 in 2010 and 22 in 2019 (Supplementary data, File S1, Table S4[2]). The notable changes in species presence were as follows: *H. alpina* was consistently present starting in 2016;

Fig. 2. Abiotic variable change over years at both Atqasuk (red line) and Utqiaġvik (blue line) for average air temperature (°C), average thaw depth (cm), average volumetric water content, thawing degree day sums, average soil temperature (°C), and sum of precipitation (cm).
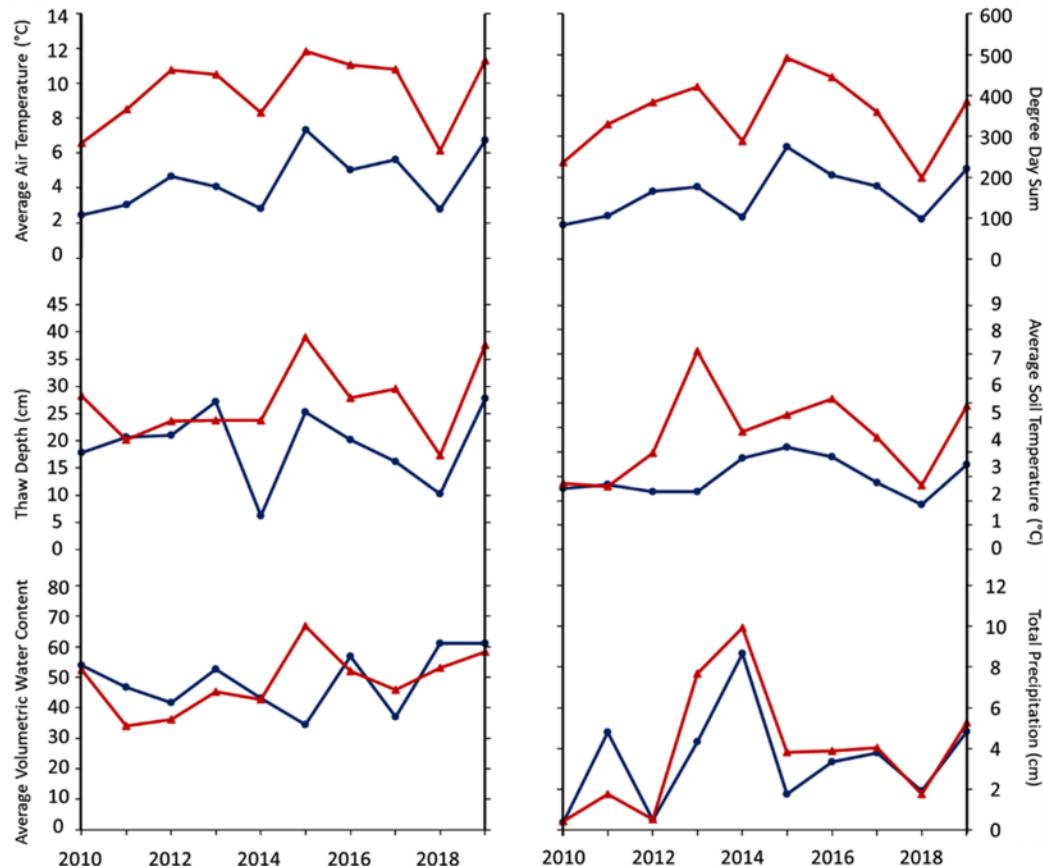
**Fig. 3.** Cover change over years at both Atqasuk and Utqiaġvik.
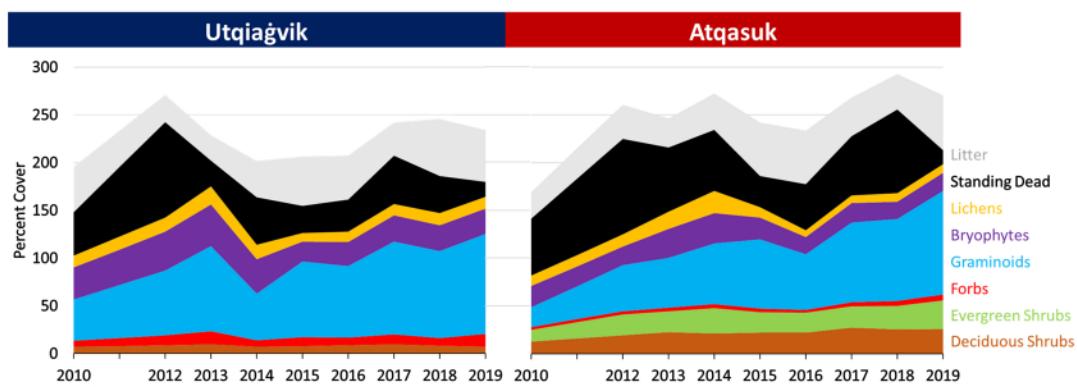
Table 1. Change in vascular plant diversity at Atqasuk and Utqiaġvik between 2010 and 2019. Alpha, beta, Shannon and Evenness diversity indices were calculated for each plot ($n = 30$); the average index value and the standard deviation (in parentheses) are presented.

	2010	2012	2013	2014	2015	2016	2017	2018	2019	r^2
Atqasuk grid										
Alpha	5.77 (2.14)	5.53 (2.08)	5.63 (2.03)	5.83 (2.02)	6.30 (1.84)	5.13 (1.74)	6.00 (2.20)	6.07 (2.30)	5.70 (1.84)	0
Beta	0.22 (0.08)	0.22 (0.08)	0.23 (0.08)	0.23 (0.08)	0.25 (0.07)	0.21 (0.07)	0.23 (0.08)	0.23 (0.09)	0.26 (0.08)	0.01
Gamma	26	25	25	25	25	24	26	26	22	0.88
Shannon	1.34 (0.45)	1.27 (0.41)	1.27 (0.41)	1.29 (0.44)	1.29 (0.38)	1.20 (0.41)	1.27 (0.39)	1.21 (0.44)	1.23 (0.39)	0.01
Evenness	**0.81 (0.12)**	**0.79 (0.11)**	**0.79 (0.12)**	**0.76 (0.17)**	**0.72 (0.15)**	**0.77 (0.12)**	**0.75 (0.13)**	**0.70 (0.19)**	**0.72 (0.13)**	**0.04**
Utqiaġvik grid										
Alpha	7.30 (2.51)	6.77 (2.31)	8.13 (2.62)	7.23 (2.67)	7.60 (2.59)	6.63 (2.63)	7.93 (3.02)	6.43 (2.34)	7.33 (2.51)	0
Beta	0.25 (0.09)	0.27 (0.09)	0.27 (0.09)	0.27 (0.10)	0.24 (0.08)	0.24 (0.09)	0.26 (0.10)	0.25 (0.09)	0.25 (0.09)	0
Gamma	29	25	30	27	32	28	30	26	29	0.32
Shannon	**1.42 (0.45)**	**1.30 (0.37)**	**1.41 (0.39)**	**1.36 (0.39)**	**1.30 (0.35)**	**1.24 (0.36)**	**1.30 (0.33)**	**1.23 (0.34)**	**1.28 (0.32)**	**0.02**
Evenness	0.72 (0.15)	0.70 (0.13)	0.68 (0.11)	0.71 (0.11)	0.66 (0.14)	0.68 (0.13)	0.65 (0.10)	0.68 (0.12)	0.67 (0.12)	0.01

Note: Gamma diversity represents the species richness for the site and is therefore a single value for each year. Linear mixed models were used to generate r^2 values for the relationship between diversity metrics and years; significant relationships are indicated in bold font. A listing of each species sampled each year is available in the Supplementary data (File S1, Table S2[2]).

Fig. 4. Height change of functional groups over years in Atqasuk and Utqiaġvik.
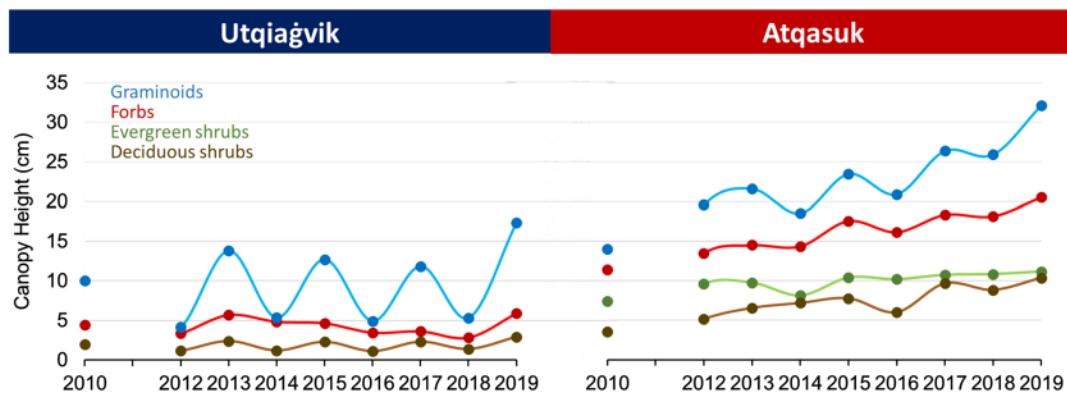
Luzula wahlenbergii disappeared from plots starting in 2016; *Carex rariflora, Diapensia lapponica, Juncus biglumis, Lloydia serotina, Oxyria digyna, Poa arctica, Poa viviparum,* and *Potentilla hyparctica* were intermittently present depending on the year. In Utqiaġvik, the values for gamma diversity were 29 in 2010 and in 2019 (Supplementary data, File S1, Table S4[2]). The notable changes in species presence were as follows: *Festuca brachyphylla* and *Stellaria humifusa* appeared less frequently in later years; *Pedicularis lanata, P. sudetica, P. hyparctica, Ranunculus nivalis,* and *Ranunculus pallasii* appeared more frequently in later years; *Calamagrostis holmii, Draba lactea,* and *Ranunculus pygmaeus* were intermittently observed depending on the year. The data used may be found in the Supplementary data, Files S4 and S5[2].

Vegetation height

At Atqasuk, the heights of all functional groups increased over years: deciduous shrubs, from 11.5 to 20.5 cm, $r^2 = 0.11$; evergreen shrubs from 7.4 to 11.2 cm, $r^2 = 0.04$; forbs from 3.6 to 10.4 cm, $r^2 = 0.19$; and graminoids from 14.0 to 32.1 cm, $r^2 = 0.21$ (Fig. 4; Supplementary data, File S1, Table S5[2]). The growth height of the following species also increased with time (years): *B. nana, S. pulchra, Cassiope tetragona, Ledum palustre, V. vitis-idaea, R. chamaemorus, C. aquatilus, C. bigelowii, E. russeolum, E. vaginatum,* and *Trisetum spicatum.* At Utqiaġvik, graminoids were the only functional group that increased in growth height over time (from 10.00 to 23.10 cm, $r^2 = 0.21$) (Fig. 4; Supplementary data, File S1, Table S5[2]). The growth height of the following species also increased with time (years): *Salix rotundifolia, Petasites frigidus, Saxifraga cernua, Arctagrostis latifolia, Carex stans, Dupontia fisheri, E. russeolum, E. triste, L. confusa,* and *P. arctica.* The data used may be found in the Supplementary data, Files S6 and S7[2].

Drivers of change

At Atqasuk and Utqiaġvik, plant cover was most closely associated with year, soil temperature, and soil moisture (Table 2). At Atqasuk, all taxa of vascular plants, except *Cassiope tetragona* and *Ledum palustre,* showed a relationship with year, whereas bryophytes and lichens did not, and were instead more likely to show a relationship with soil moisture. At Atqasuk, cover for many vascular taxa and pleurocarpous mosses was associated with soil temperature. Especially noticeable was a 5-fold increase in graminoid cover at Atqasuk over the 10 years studied. At Utqiaġvik, there were fewer relationships; the only generalization to be made was that graminoids generally showed a relationship with year.

Table 2. The relationship between vegetation cover and abiotic factors at Atqasuk and Utqiaġvik.

	Year	Air temp. (avg.)	Air temp. (max.)	Degree day (sum)	Soil temp. (avg.)	Soil temp. (max.)	Thaw depth (avg.)	Precip. (sum)	Soil moist. (avg.)
Atqasuk grid									
Deciduous shrub	**1289**	1291	1185	1290	1185	1290	1153	1290	**1288**
Betula nana	**846**	847	772	846	771	847	749	847	848
Salix pulchra	**582**	585	536	584	537	584	542	585	586
Evergreen shrub	**1428**	1427	1258	1427	**1255**	1427	1287	1428	**1410**
Cassiope tetragona	618	619	562	619	562	615	559	618	620
Ledum palustre	1055	1055	926	1055	926	1054	945	1054	**1040**
Vaccinium vitis-idaea	**1047**	1047	944	8575	944	1046	930	1047	**1043**
Forb	**813**	815	733	815	**729**	813	733	814	816
Rubus chamaemorus	**518**	522	471	522	**466**	522	477	522	521
Graminoid	2781	2779	**2477**	2782	2461	2782	2457	2781	2781
Carex aquatilis	1446	1447	**1251**	1449	**1247**	1448	**1238**	1448	**1445**
Carex bigelowii	**277**	597	543	792	543	596	540	596	**592**
Eriophorum angustifolium	**478**	480	**438**	480	440	480	439	480	484
Eriophorum russeolum	**636**	636	585	636	585	635	567	635	637
Eriophorum vaginatum	**1177**	1176	1059	1177	1059	1175	1078	1175	**1169**
Trisetum spicatum	577	578	**465**	578	471	578	541	577	579
Bryophyte	2336	2334	2127	2339	**2123**	2337	2092	2336	2337
Acrocarpous moss	1553	1551	1358	1551	1358	1550	**1369**	1550	1554
Pleurocarpous moss	983	985	**834**	984	**817**	985	**894**	983	**974**
Lichen	1254	1255	1092	1254	1093	1254	1133	1254	**1241**
Crustose	327	327	287	327	289	327	235	327	329
Foliose	839	839	745	840	747	839	731	839	**837**
Fruticose	1081	1081	959	1187	959	1081	965	1080	**1069**
Standing dead	3646	3649	3249	3761	3248	3647	**3217**	3647	3654
Leaf litter	**2942**	2944	**2697**	2940	**2695**	2940	2552	2942	**2911**

Table 2. (*concluded*).

	Year	Air temp. (avg.)	Air temp. (max.)	Degree day (sum)	Soil temp. (avg.)	Soil temp. (max.)	Thaw depth (avg.)	Precip. (sum)	Soil moist. (avg.)
Utqiaġvik grid									
Deciduous shrub	713	713	713	713	**633**	635	711	713	712
Salix pulchra	183	183	183	183	173	172	183	182	**183**
Salix rotundifolia	689	689	688	689	614	614	689	689	690
Forb	1562	1563	1561	1560	**1339**	**1328**	**1535**	1562	1566
Petasites frigidus	**623**	**622**	**623**	**622**	551	550	625	622	622
Stellaria laeta	562	562	563	563	498	497	557	562	**561**
Graminoid	**2715**	2714	2713	2716	2445	2449	2721	2716	2721
Arctagrostis latifolia	**567**	569	568	569	514	516	571	569	570
Carex stans	1820	1820	**1818**	1819	1656	1653	1825	1819	1822
Dupontia fisheri	1516	1514	1514	1513	1341	1341	1520	1515	**1515**
Eriophorum russeolum	**1561**	1560	**1558**	1560	1356	1355	1565	1561	1566
Eriophorum triste	**1408**	1406	1409	1408	1259	1256	1421	1411	1414
Luzula arctica	**480**	481	481	481	**428**	431	480	481	**476**
Luzula confusa	703	703	702	702	640	634	706	702	706
Poa arctica	1191	1188	1189	1189	1044	1046	**1183**	1189	**1186**
Bryophyte	2978	2976	2980	2979	**2620**	**2614**	**2971**	2976	2985
Acrocarpous moss	**2261**	2268	**2263**	2266	**1800**	**1800**	2268	2264	2276
Pleurocarpous moss	2068	2067	2067	2068	1818	1811	2071	2065	2075
Lichen	1203	1203	1204	1203	1081	1080	1204	1203	1204
Foliose	863	865	863	864	767	763	866	863	868
Fruticose	949	948	949	949	860	860	948	950	950
Standing dead	3788	3792	3791	3790	3358	3358	3801	3789	**3794**
Leaf litter	3047	3047	3049	3047	**2778**	**2771**	**3031**	3049	**3048**

Note: Values represent the widely applicable information criterion (WAIC) from Bayesian regression models between cover groups. WAIC values were determined after regressing a single log linked cover group variable to every other functional group sequentially. Values can be compared horizontally with lower numbers indicating a better fit. A Poisson distribution was assumed. Plot location ($n = 30$) was considered a source of random error. Column and row headers indicate abiotic factors and functional group respectively. WAIC values from significant models are indicated in bold font.

At Atqasuk and Utqiaġvik, the growth height of vascular plants was associated with year (Table 3). At Utqiaġvik, there were also a number of relationships with air temperature.

Discussion

The vegetation of the Arctic is changing (Frost et al. 2020). Graminoid cover increased 5-fold at Atqasuk over 10 years; graminoid cover also increased at Utqiaġvik. Changes in vegetation cover over time in Arctic communities are important to document because plant community composition can greatly influence the overall energy balance of tundra ecosystems. The energy balance of tundra ecosystems is crucial for ecosystem processes, such as carbon and nutrient cycling, plant growth and productivity, and microbial activity (Lund et al. 2014). Woody species (i.e., deciduous and evergreen shrubs) have been shown to greatly alter belowground carbon exchange rates (Parker et al. 2020); thus, dramatic increases in the cover of woody species have the potential to greatly alter ecosystem structure and function. Additionally, encroachment of tall-statured shrubs shades neighboring plants, which has been shown to restrict plant growth (Graglia et al. 1997).

Increases in shrub and graminoid cover affect more than plant–plant interactions. Shading imposed from neighboring shrubs has been shown to delay flowering, which could reduce (or eliminate) pollinator visitation and (or) berry production (Hoye et al. 2013). Changes in berry production could affect the populations of mammalian and avian species that rely on berries as a food source. Graminoids and deciduous shrubs are the primary food sources for most Arctic herbivores. Long-term herbivore exclusion experiments have shown that the absence of herbivory (i.e., lemmings, caribou) greatly alters several ecosystem properties, including labile soil nitrogen, thaw depth, water table, and CH_4 exchange (Lara et al. 2017; Sundqvist et al. 2019). The presence of herbivores has also caused a shift in community composition in wet meadow communities, from predominately graminoids to mosses (Lara et al. 2017). In a short-term Tibetan alpine meadow, Liu et al. (2017) demonstrated that the phenology of common forbs was sensitive to both mowing and nitrogen addition. Enhanced nitrogen levels in soils delayed flowering events by approximately a week and half, while mowing and nitrogen additions hastened the first and last flowering times by as much as a week. Herbivory in increasingly nutrient rich tundra facilitated by increasing thaw depths may cause plant phenology to accelerate for tundra species. More research is needed to understand the various trophic cascades associated with shifts in vegetation community composition, but documenting vegetation change over time and in response to warming is the first step to understanding how the Arctic is responding to a warming climate (Post and Forchhammer 2008).

Species diversity (both Shannon's index and Pielou's evenness) declined at both sites over time, owing to a disproportionate increase in the abundance of species. Measures of species richness (alpha, beta, and gamma diversity) did not change. Declines in species diversity contradict previous studies showing increased species diversity over time (Villarreal et al. 2012; Lokken et al. 2020) and the general pattern of increased diversity at warmer locations (Walker 1995). Because species diversity is a function of species evenness, increases in cover for the dominant species without the addition of newly introduced species would cause an overall decrease in diversity. Because the study sites span a wide range of community types, it is unlikely that a 30-plot sample is sufficient to capture all species present in the surrounding area. Previous studies, which focused on one or two community types, showed increased species richness (gamma diversity) over time as the abiotic conditions (e.g., soil moisture, soil temperature, etc.) changed, and new species, including nearby species that were simply absent from plots, migrated into the plots. Another consideration when determining trends in species diversity is whether the species in question were either uncommon or rare at the beginning of the study. For instance, while *P. arctica* was

Table 3. The relationship between plant height (by growth form and species) and abiotic factors at Utqiaġvik and Atqasuk.

	Year	Air temp. (mean)	Air temp. (max.)	Degree day (sum)	Soil temp. (mean)	Soil temp. (max.)	Thaw depth (mean)	Precip. (sum)	Soil moist. (mean)
Atqasuk grid									
Deciduous shrub	**0.11**	0.02	0.03	0.01	0.00	0.00	0.02	0.00	0.00
Betula nana	**0.07**	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00
Salix pulchra	**0.31**	0.03	0.08	0.01	0.02	0.01	0.10	0.00	0.00
Evergreen shrub	**0.04**	0.01	**0.02**	0.01	**0.04**	**0.03**	0.00	0.00	0.00
Cassiope tetragona	**0.03**	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Ledum palustre	**0.05**	0.00	0.02	0.00	**0.04**	0.02	0.00	0.00	0.00
Vaccinium vitis-idaea	**0.10**	0.04	0.05	0.02	0.00	0.00	0.01	0.00	0.00
Forb	**0.19**	0.02	0.03	0.00	0.02	0.01	0.02	0.02	0.00
Rubus chamaemorus	**0.30**	0.03	0.06	0.00	0.02	0.02	**0.08**	0.00	0.00
Graminoid	**0.21**	0.04	**0.09**	0.01	**0.03**	**0.02**	0.02	0.00	**0.01**
Carex aquatilus	**0.31**	0.04	0.09	0.01	**0.04**	**0.03**	**0.04**	0.00	**0.03**
Carex bigelowii	**0.15**	0.02	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Eriophorum russeolum	**0.44**	0.05	0.11	0.02	**0.10**	**0.12**	0.04	0.06	0.00
Eriophorum vaginatum	**0.18**	0.05	**0.13**	0.02	0.00	0.00	0.01	0.01	0.00
Trisetum spicatum	**0.30**	0.03	0.08	0.00	0.02	0.00	0.17	0.01	0.00
Utqiaġvik grid									
Deciduous shrub	0.06	0.04	0.03	0.02	0.01	0.01	0.00	0.00	0.00
Salix pulchra	0.02	0.06	**0.10**	**0.07**	0.02	0.01	0.00	0.05	0.00
Salix rotundifolia	**0.08**	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.00
Evergreen shrub	—	—	—	—	—	—	—	—	—
Forb	0.04	0.05	**0.05**	**0.03**	0.00	0.00	0.02	0.00	0.01
Petasites frigidus	**0.05**	0.04	**0.04**	0.02	0.00	0.00	0.02	0.00	0.05
Saxifraga cernua	**0.16**	0.09	**0.18**	0.07	0.08	0.06	0.00	0.04	0.00
Stellaria laeta	0.05	**0.15**	**0.12**	**0.10**	0.00	0.00	0.05	0.00	0.03
Graminoid	**0.21**	**0.14**	**0.14**	0.09	0.00	0.00	0.00	0.00	**0.01**
Arctagrostis latifolia	**0.20**	0.05	0.05	0.02	0.00	0.02	0.08	0.00	0.01
Carex stans	**0.20**	**0.11**	**0.11**	0.06	0.00	0.00	0.00	0.00	**0.01**
Dupontia fisheri	**0.26**	**0.24**	**0.24**	**0.17**	0.00	0.00	0.00	0.00	0.00
Eriophorum russeolum	**0.39**	**0.18**	**0.22**	0.12	0.01	0.01	0.01	0.00	0.00
Eriophorum triste	**0.34**	**0.21**	**0.22**	0.13	0.00	0.00	0.01	0.01	0.00
Luzula arctica	0.00	0.07	0.06	0.06	0.03	0.09	0.12	0.01	**0.19**
Luzula confusa	0.11	0.10	**0.13**	**0.10**	0.11	0.14	0.17	0.00	0.00
Poa arctica	**0.12**	**0.14**	**0.12**	**0.10**	0.01	0.03	0.00	0.00	0.00

Note: Values represent marginal r^2 values from general linear mixed models regressing functional group average max height with abiotic factors including time. Plot location and year were considered sources of random error (*n* varies by functional group and site, see the Supplementary data, File S1, Table S5[2]). Column headers indicate abiotic variables and row headers indicate broad functional groups. Values in bold font represent significant effects.

widespread over the Utqiaġvik ARCSS grid, its distribution over the Atqasuk ARCSS grid was quite low, even at the beginning of the observation period, appearing only in 2015 in Atqasuk (Supplementary data, File S1, Table S4[2]). Over longer observation periods, it is likely that new species will invade both regions and reverse the observed trend of the decline in species diversity at the sites. Additionally, more intense herbivory could influence this trend: caribou can cause declines in lichen populations (Bernes et al. 2015; Sundqvist et al. 2019); reindeer exclusion experiments have shown that plants with low stature and low leaf area experience declines in the absence of grazing (Kaarlejarvi et al. 2017). While grazing tends to increase species diversity, it could be offset by soil nutrient inputs, such as nitrogen, which may increase as a result of herbivory (Borer et al. 2014; Kaarlejarvi et al. 2017). Signs of intense grazing are neither obvious nor well quantified at the plot level, and are a focus of future investigation.

The increase in plant cover observed in this study, particularly at Atqasuk, is consistent with the recent greening of the North Slope of Alaska, which has been detected by satellite observations (Frost et al. 2020). Other studies have attributed green trends with changes in photosynthetic biomass, green leaf area index (LAI), plant cover, and vegetation productivity (Jia et al. 2009; Forbes et al. 2010; Beck and Goetz 2011; Epstein et al. 2012; Bhatt et al. 2013; Pattison et al. 2015; Ju and Masek 2016; Kobayashi et al. 2018; Walther et al. 2018). Greening trends across the Arctic are complex, and not all studies come to the same conclusions (Beamish et al. 2020; Myers-Smith et al. 2020), and a disagreement between sensing platforms and approaches has been observed (Guay et al. 2014). Common spectral indices used to detect vegetation, such as the normalized difference vegetation index (NDVI), have been shown to be sensitive to nonvegetation landscape features such as water in saturated tundra, snow cover, and even shadow (Gamon et al. 2013; Raynolds et al. 2013; Pattison et al. 2015). Additionally, plant moisture content, such as the moisture in sphagnum moss mounds, can drastically alter NDVI by as much as 80%, depending on moisture levels (May et al. 2018). Therefore, it is essential that vegetation monitoring be coupled with remote sensing to understand the drivers of change.

Drivers of vegetation change

Overall, the best predictors for change in either cover or growth height were year, soil temperature, soil moisture, or air temperature. The strong relationship between plant cover and plant growth height with year implies a cumulative response to regional climate warming. The correspondences between vegetation cover, soil moisture, and temperature of the current year's growing season suggests considerable plasticity in overall tundra vegetation growth between years (Walker et al. 1994; van der Wal and Stien 2014). Biomass in tundra regions has been linked to soil temperature (Hill and Henry 2011; Natali et al. 2012). Soil moisture and precipitation are known constraints on the growth of Arctic vegetation (Chapin et al. 1996; Blok et al. 2011). In our study, precipitation was a modest predictor of cover change, but did not successfully predict changes in growth height. Soil moisture was an important predictor in Atqasuk, and a modest predictor of cover change in Utqiaġvik, as well as a modest predictor of height change at either site. This is reasonable, given that past work has indicated that soil moisture is a limiting factor for vegetation growth (Chapin et al. 1995; Gamon et al. 2013; Botting 2015). Thaw depth was a modest predictor of cover change at either research site and was not as well-represented as soil temperature for predicting plant height change at either site, although thaw depth was associated with community composition and growth (Schuur et al. 2007; Lantz et al. 2009). It would be beneficial for future studies to discern the best groups of predictors for broad functional groups and the most common taxa, via multivariate modeling on this dataset.

Comparison between regions

The larger documented change at the lower Arctic site, Atqasuk, relative to the higher Arctic site, Utqiaġvik, is consistent with previous studies that found greater changes in the cover of shrubs at warmer locations (Walker et al. 2006; Elmendorf et al. 2012). While Utqiaġvik is considered a coastal low Arctic subzone C site, it may slowly transition to more resemble low arctic subzone D communities if erect shrubs become more dominant, and an influx of southern species that are better adapted to warm weather move in; anecdotal evidence indicates the presence of several *Salix* species present in the region, which were not sampled during the 1980s (Murray and Murray 1978). Global monitoring networks across the tundra biome have shown a general increase in the stature of most tundra plants and consistent increases in cover over time (particularly for shrubs), which is consistent with our own findings (Elmendorf et al. 2012; Bjorkman et al. 2018; Myers-Smith et al. 2019; Bjorkman et al. 2020).

Our results are consistent with experimental warming studies that have shown an increase in shrub and graminoid cover with temperature at other tundra locations (Callaghan et al. 2011; Elmendorf et al. 2012; Bjorkman et al. 2020) and at adjacent sites at Atqasuk and Utqiaġvik, which also included an increase in canopy height (Hollister et al. 2015). Increases in the heights of graminoids in Utqiaġvik and of graminoids and shrubs in Atqasuk are consistent with findings from other research that showed with warming and time, graminoids increase in height in cooler regions and deciduous shrubs increase in height in warmer regions (Elmendorf et al. 2012; Jorgenson et al. 2015). A similar long-term monitoring study on Qikiqtaruk-Herschel Island in Canada found that average canopy height doubled from 1999 to 2017, and that tundra shrub height increased and was driven by sensitivity to summer growing temperatures (Myers-Smith et al. 2019). The one notable exception is warming experiments often show a decline in bryophytes and lichens as vascular plants increase; here, we show considerable variability in the cover of these taxa, with the only significant change being a decline in acrocarpous mosses at Utqiaġvik. Jorgenson et al. (2015) noted decreases in the cover of acrocarpous mosses in a low Arctic study in the Arctic National Wildlife Refuge, while the cover of other bryophytes remained unchanged, suggesting that a decline in acrocarpous mosses may be common in more than one coastal Arctic ecosystem. Findings from warming experiments in plots adjacent to this study in Utqiaġvik and Atqasuk also suggest that the lack of a consistent decrease in bryophyte and lichen cover is likely due to considerable variability in cover between years (Hollister et al. 2015). Given that the average cover of vascular plants has only approached full cover (100%) in the past few years, and there is a considerable amount of open ground, it is therefore possible that vascular plants have not yet imposed considerable shading or considerable levels of other adverse effects, such as decreasing nutrient availability, on nonvascular plants. Inconsistent trends in bryophyte cover could also be attributed to fluctuations in lemming populations, particularly at Utqiaġvik, which have been shown to drastically reduce graminoid cover and promote bryophyte cover (Lara et al. 2017). Herbivory coupled with sensitivity to even small fluctuations in temperature (Hollister et al. 2015) may explain much of the interannual variability in tundra vegetation cover (Johnson et al. 2011). Additionally, although not a focus of this study, there has been noticeable ice-wedge degradation around a few plots, which may have contributed to changes in plant cover or growth height.

The cover of standing dead plants and leaf litter were somewhat inverse to each other at both sites (Supplementary data, File S1, Table S1[2]). Other studies have indicated that standing dead cover fluctuates between years as a function of leaf retention time (Knapp and Seastedt 1986) and herbivory, especially during years with large populations of lemmings (Villarreal et al. 2012). Both processes may account for the increase in leaf litter.

It is probable that, at least for our study site (Atqasuk), much of the increase in leaf litter could be attributed to the large increase in graminoid cover. Standing dead and leaf litter cover are important to include in vegetation cover change studies because they influence the composition of the surrounding plant community and the overall productivity of the ecosystem (Knapp and Seastedt 1986). Leaf litter accumulation coupled with increased temperatures over time also influences decomposition rates, which has the potential to alter the rate of carbon exchange, and therefore the overall carbon budget, in the tundra (McLaren et al. 2017; Parker et al. 2018).

There are several sources of uncertainty that have not already been noted in this study. Despite sampling each plot within the same 14 day-of-the-year range across years, vegetation measurements were spread across the season and the frequency of abiotic measurements was up to a 2-week interval. The asynchrony between measurements can mask the associations. For example, within-season variability in moisture levels, especially for mosses, can influence cover estimates, and early sampling during a cold summer or later sampling during a warm dry year could contribute to annual differences. Lastly, there is evidence that the nongrowing season temperature may be an important determinant of plant productivity (Miao et al. 2020), which was not addressed in this study, and we did not account for the cumulative effects of previous years on each year (van der Wal and Stien 2014).

Conclusions

Our results show that the plant cover and plant height increased from 2010 to 2019 at our two research sites, which were distinguished by climatic factors and geographical distance. While plant cover and growth height were associated with many abiotic factors such as soil moisture and soil temperature, most of the changes in vegetation were best predicted by year. At both sites, significant cover change was driven by shifts in species within the genera *Carex* and *Eriophorum*. In Atqasuk, there was more cover change in shrubs than in Utqiaġvik. Diversity indices at both sites indicated that species evenness decreased over the monitoring period. Given the similarity of these changes between sites and the consistency of findings with adjacent warming experiments (Hollister et al. 2015), it is likely that the increase in plant cover at both sites is the result of regional climate warming.

Documenting and understanding vegetative and environmental changes is important for many reasons. Successfully predicting changes as natural communities experience climate change will allow researchers and natural resource managers to better maintain ecosystem services and natural resources. To understand the bottom-up effects within ecosystems, it is necessary to understand the plant community. Plant community metrics, such as cover and height, are useful for understanding the influence of competition, albedo, and habitat suitability. An ever-evolving awareness of how environmental abiotic factors influence the characteristics of plant communities across the Arctic is necessary to develop more useful models for predicting changes. It would be useful to develop a multivariate set of models to predict changes that may integrate phenological and plant trait observations with vegetation cover. Additionally, investigating whether satellite or aerial imagery corroborates our findings at these sites would be helpful for better understanding the changes in and around the greater region.

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Author contributions

J.H. wrote the manuscript, performed all statistical analyses, and collected vegetation cover measurements; R.H. helped to provide funding for the study, helped co-write the manuscript, and assisted with data analyses; T.B. helped to formulate the study design and collected the vegetation cover measurements; C.T. helped to provide funding for the study, contributed abiotic data, and revised the manuscript; K.B. helped to write the manuscript and collected vegetation cover measurements; J.M., R.B., and J.L. established the current vegetation plots, led early vegetation cover measurements, and revised the manuscript; H.C. collected vegetation cover measurements and revised the manuscript; S.V., M.O., and T.F. collected the abiotic measurements and revised the manuscript.

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