Plot-scale evidence of tundra vegetation change and links to recent summer warming

Sarah C. Elmendorf, Gregory H. R. Henry, Robert D. Hollister et al.*

Temperature is increasing at unprecedented rates across most of the tundra biome¹. Remote-sensing data indicate that contemporary climate warming has already resulted in increased productivity over much of the Arctic^{2,3}, but plot-based evidence for vegetation transformation is not widespread. We analysed change in tundra vegetation surveyed between 1980 and 2010 in 158 plant communities spread across 46 locations. We found biome-wide trends of increased height of the plant canopy and maximum observed plant height for most vascular growth forms; increased abundance of litter; increased abundance of evergreen, low-growing and tall shrubs; and decreased abundance of bare ground. Intersite comparisons indicated an association between the degree of summer warming and change in vascular plant abundance, with shrubs, forbs and rushes increasing with warming. However, the association was dependent on the climate zone, the moisture regime and the presence of permafrost. Our data provide plot-scale evidence linking changes in vascular plant abundance to local summer warming in widely dispersed tundra locations across the globe.

Latitudinal gradients in tundra vegetation and palaeorecords of increases in the abundance of tundra shrubs during warm periods provide strong evidence of climate warming as an important moderator of plant composition in this biome⁴. The long life span of most tundra plants suggests that community-level responses to environmental change could occur over decades to centuries, but several lines of evidence indicate that climate-induced changes in tundra vegetation may already be detectable, portending more drastic changes in the coming decades. First, a systematic resurvey of European alpine plants found detectable decreases in cold-adapted species and increases in warm-adapted species over a five-year period, and that such changes were correlated with the degree of localized warming⁵. Second, warming experiments across the tundra biome have documented impacts of a 1-2°C increase in summer temperature on the composition of tundra plant communities within a decade of warming in some regions, but also highlighted the resistance of tundra vegetation composition to climate warming in some locations^{6,7}. Third, normalized difference vegetation index (NDVI) values have increased over the tundra biome in recent years, indicating a greening of the tundra ecosystem coincident with climate warming trends^{2,3}. However, NDVI values are sensitive to a variety of ground-cover changes that can be difficult to tease apart, such as the amount and type of vegetation, litter, bare ground and soil-moisture status, and potentially influenced by non-vegetation changes such as atmospheric conditions and satellite drift⁸. Last, plotbased sampling, repeat aerial photography and annual-growth-ring studies have documented recent increases in biomass and shrub abundance in many, but not all, Arctic, high-latitude and alpine tundra ecosystems⁹⁻¹³. Attributing these results to climate patterns in a single region is tenuous because factors other than climate

could be responsible for the observed changes. Thus, despite these compelling lines of evidence, uncertainty remains as to the extent of change in vegetation that has occurred across the tundra biome owing to climate change.

Cross-study synthesis offers an opportunity to take advantage of naturally occurring spatial variation in the rate and direction of climate change to test the association between site-specific environmental and biological change¹⁴. Here, we report on decadal scale vegetation changes that have occurred in Arctic and alpine tundra using the largest data set of plot-level tundra vegetation change ever assembled (Fig. 1; Supplementary Table S1). We hypothesized that tundra vegetation is undergoing directional change over time, with an increase in canopy height and abundance of vascular plants, particularly deciduous, tall and low-growing shrubs, and a corresponding decline in mosses, lichens and bare ground, similar to what has been observed in tundra warming experiments^{6,7}. We anticipated that these changes would be greatest in the areas with the most pronounced increases in summer air temperature. Therefore, we examined biome-wide trends in vegetation change; whether vegetation change was spatially associated with local summer temperature trends; and whether the direction of observed changes was consistent with predictions based on warming experiments in tundra ecosystems.

Across studies we found increases in mean canopy height; increases in the maximum height of shrubs (especially deciduous, dwarf and tall shrubs), graminoids (especially grasses) and forbs (Fig. 2a); increases in the abundance of litter and evergreen, low and tall shrubs; and declines in bare ground cover (Fig. 2b). Although not always statistically significant, general trends in the height and abundance of vascular and non-vascular plant groups were largely congruent with expectations based on warming experiments; litter and most vascular growth forms increased in height and abundance, whereas mosses showed decreasing trends. These patterns also align with satellite-derived observations of greening across the tundra biome, which are typically thought to reflect increases in total photosynthetic biomass¹⁵, leaf area¹⁶ and shrub biomass¹⁷.

Summer temperature increased significantly over the study region, but the rate of change was spatially variable: mean study-period summer warming = $0.72 \,^{\circ}C$ (standard error (s.e.m.) = 0.10); p < 0.0001 based on generalized estimating equations (GEEs), range = $-1.47-2.29 \,^{\circ}C$. Taking advantage of the variability among studies, we compared local patterns of vegetation change with local temperature records to determine the sensitivity of tundra vegetation to summer temperature change.

Although shrubs are thought to be increasing over much of the tundra biome, we did not find that all types of shrub were uniformly increasing where the summer climate was warming. Instead, we found that warming had a positive effect on the total abundance of shrubs primarily in study locations that were warmer to begin with (Supplementary Table S2; Fig. 3a),

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Figure 1 | **Study site locations.** Study sites spread across the tundra biome in the Arctic, alpine and Antarctic regions. Black symbols represent the grid-cell centres of the 46 locations into which the 158 studies were grouped for the analysis.

a pattern that seems to be driven primarily by strong positive responses of deciduous shrubs to warming in relatively warm tundra regions (Supplementary Table S2; Fig. 3d). We also found that tall and low-growing but not dwarf or evergreen shrubs increased in abundance with summer climate warming throughout the study area (Supplementary Table S2; Fig. 3b,c) and that deciduous shrub increases were most positively associated with warming on wet sites (Supplementary Table S2; Fig. 3d). These patterns largely align with results from long-term warming experiments, in which total and deciduous shrub expansion was stimulated by warming treatments only in warm tundra regions with moist to wet soils, tall shrubs increased with experimental warming throughout their range and dwarf shrubs decreased with experimental warming⁷. On a landscape level, our results are also supported by an analysis of NDVI trends over Canada, where pixels with significant greening trends were concentrated in the low Arctic and subArctic zones³.

Responses of other plant groups were not as strong and consistent as those of shrubs and they differed somewhat from predictions based on long-term warming experiments (Supplementary



Figure 2 | **Biome-wide changes in vegetation height and abundance.** Biome-wide changes in vegetation height (**a**) and abundance (**b**) of each vegetation response group. Vegetation height is expressed as the plot canopy mean and the maximum of each taxon and abundance is expressed as the probability of increase. Error bars show ± 2 s.e.m. based on intercept-only GEEs and are emboldened where mean change rates were significant at *P* < 0.05 using Wald tests. Sample sizes (number of studies, number of locations) and response groups are indicated on the *x* axis.

Table S2). We found that increases in forbs were correlated with summer temperature trends, but only for study sites with nearsurface permafrost (Fig. 3e). Rushes increased in warming regions, but only in wet sites (Fig. 3f), although this finding is somewhat tenuous given that rushes are typically uncommon (comprising <5% of total vegetation) and therefore prone to increased sampling error. Surprisingly, although we found significant overall increases in litter over time, there was no strong association between climate warming and litter accumulation. Shrubs are known to produce relatively recalcitrant litter, but it is possible that the decomposition of litter was promoted by warming, such that there was no net accumulation¹⁸. There was also no indication that summer climate warming was driving declines in lichens and mosses, despite welldocumented links between summer temperature and cryptogam abundance from both experimental and gradient studies^{6,7,19}. This result may be tied to the absence of litter build-up in warming regions, as the negative effects of warming on cryptogams are thought to be an indirect result of shading and litter deposition²⁰. Furthermore, these groups are known to be especially sensitive to soil moisture and snowmelt, and any direct effects of temperature may have been masked by local changes in moisture availability and growing-season length²¹.

Recently published studies linking changes in the abundance⁵ and range limits¹⁴ of individual species to local warming trends provide compelling evidence that climate change influences species diversity and distribution. Our data indicate that summer climate warming is also altering the physiognomic structure of tundra communities. These findings are particularly consequential in light of how shrub cover alters both abiotic (faster snow melt, higher sensible heat flux during snowmelt, lower surface albedo, warmer winter and cooler summer soils) and biotic (abundance and diversity of understorey species, particularly lichens) conditions¹².

Although we found some directional changes across the tundra biome as a whole, understanding the drivers of these changes is complicated by the uneven distribution of the study sites

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Figure 3 | Relationship between vegetation change and summer temperature change. Vegetation change as a function of summer temperature change. **a-f**, Bands show the predicted probability of increase ± 2 s.e.m., based on GEEs where the change in vegetation response groups was significantly correlated with summer temperature change (**b**,**c**), or interactions between summer temperature change and mean summer temperature (**a**,**d**), moisture (**d**,**f**) or permafrost (**d**) (Supplementary Table S2). Raw data are superimposed as points with size corresponding to the number of individual studies with increases (top) and decreases (bottom) in abundance and coloured by site characteristics (mean summer temperature, moisture class, or presence of near-surface permafrost), where appropriate. GEEs in panels **a** and **d** were parameterized using mean summer temperature as a continuous variable; however, to visualize results graphically we generated predicted responses at only two representative summer temperatures (5 °C and 9 °C).

examined. One likely source of response heterogeneity is the variable species and growth-form composition, which partially co-vary with temperature, moisture gradients and geographic regions. For example, dwarf shrubs are most abundant in colder regions whereas tall shrub species occur more frequently in warm regions. Working on a global scale necessitated that we examine changes at the growth-form, rather than species level, as no single species was present at all sites. A potential drawback of this approach is that individual species within a growth form could respond in different ways to the same environmental perturbation²². An advantage of this approach is that tundra growth forms differ in productivity, decomposition rates, albedo and snow-catching capacity, so understanding their response to climate warming can inform models of global surface energy balance and carbon sequestration^{22,23} and generate predictions for areas beyond the monitored regions. The vast geographic distribution of the present data set yielded poor replication for the monitoring of individual species trends, but enhanced regional monitoring efforts could provide data for more robust species-level analyses. In combination with transplant experiments, these data could be used to determine whether the variation in growth-form response to warming temperatures with ambient climate and temperature is due to different resident species or genotypes²⁴, or whether factors other than summer temperature strongly limit vegetation in particular regions.

In contrast to warming experiments, which tightly control for non-temperature effects by pairing manipulated and unmanipulated treatment plots, the effects of temperature change here were evaluated across sites with a host of other potentially changing factors including anthropogenic nitrogen deposition, growingseason length, hydrology, winter and summer precipitation, disturbance regimes and grazing intensity¹³. These factors are strong drivers of tundra plant species composition^{21,25–27} that undoubtedly varied across our study sites and could show complex interactions with temperature change or themselves be changing in concert or independently of summer temperature in different tundra regions. As a result, perhaps, vegetation changes were not always tightly linked with summer temperature trends. For example, changes in moss and lichen abundance were not associated with temperature trends, and even for shrubs, numerous warming sites in warm regions actually experienced shrub declines. Similar inconsistencies have been found in correlating species distributional shifts with temperature change, where 22-25% of species' range margins moved in the opposite direction to that predicted from temperature records¹⁴. This variability emphasizes that realistic projections of future growth-form (and species) composition and abundance in tundra need to consider the relative importance of summer climate warming and other drivers of vegetation change.

This study is significant in drawing together the most complete set of information on tundra vegetation change available at present, but the distribution of sampling locations is patchy and clear knowledge gaps remain. These limitations are especially notable as future rates of surface warming are projected to accelerate beyond those that have occurred over the past few decades under almost all predicted climate scenarios²⁸. A coordinated global monitoring network that includes expansion of existing monitoring programs into systematically understudied regions and regular sampling of both biota and ecosystem processes, using standardized sampling methods, is critical for continued tracking of biotic and abiotic transitions in response to accelerating rates of tundra warming in the twenty-first century.

Methods

We surveyed plant composition in 158 plant communities in 46 locations throughout the tundra biome. Composition was measured at each study at least twice between 1980 and 2010, with a minimum of five years between the first and last survey in each study (Supplementary Table S1; Fig. 1). Methods used to quantify abundance varied among sites, which commonly occurs in global trend assessments^{29,30}. For a simple index of change that is comparable across sites, we summarized the direction of change for each growth form at each site based on the sign of the site-specific linear trend over time. We then used linear and logistic GEEs to examine biome-wide changes in canopy height, cover of bare ground, diversity and abundance of plant growth forms (Fig. 2). To account for

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spatial clustering of studies, location (determined by identity of the corresponding grid cell in the 0.5° CRU TS 3.1 (ref. 31) temperature record, which was the basis of all summer temperature-change data) was included as a grouping term with an exchangeable correlation structure³². We used the same approach to test the association between increases/decreases in vegetation groups and summer temperature change (Δ° C) over the same period³². In this analysis we also tested whether the relationship between summer temperature change and vegetation change varied depending on the mean summer temperature, soil-moisture class or underlying permafrost at the study site, as these factors have been shown to be important moderators of vegetation response to experimental climate warming. Significance of tests (based on Wald statistics, with and without correcting for multiple testing procedures) are presented in Supplementary Table S2; raw data and population-averaged trends for vegetation changes significantly associated with summer temperature change are presented in Fig. 3. We lacked height data from a sufficient number of locations for a robust comparison of local temperature trends and vegetation height changes.

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Author contributions

All authors designed and/or collected data from monitoring studies and assisted in writing the paper; S.C.E., G.H.R.H. and R.D.H. took the lead in writing the paper; S.C.E. analysed the data.

Additional information

The authors declare no competing financial interests. Data have been archived at the Polar Data Catalogue CCIN 10786. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permissions information is available online at http://www.nature.com/reprints. Correspondence and requests for materials should be addressed to S.C.E.

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Plot-scale evidence of tundra vegetation change and links to recent summer warming

FULL METHODS (Supplement)

Sources of vegetation data:

Data on changes in tundra plant composition at the plot level were amassed from a variety of sources including monitoring studies and control-plots from long-term experiments. Criteria for inclusion were permanently located quadrats or study areas which were sampled using the same methodology at least twice between 1980 and 2010 with a minimum of 5 years between the first and last sampling years. We omitted studies in areas undergoing obvious recovery from recent disturbance and plots with standing water, since it was difficult to sample submerged vegetation accurately. The resulting dataset consisted of 158 studies (Table S1). Studies were grouped into 46 locations; each location was associated with a unique 0.5 x 0.5 degree grid cell in the CRU TS 3.1 climate data set¹. The median duration of observational record per study was 11 years (range 5-27). The median number of samplings per study was 3 (range 2-28). Since the individual studies were conducted for a variety of purposes, sampling methodology varied among studies. Eighty-two percent of the studies collected vegetation data on one-to-many permanently-marked quadrats or transects within the study area; the remaining studies sampled randomly placed quadrats within a permanently-marked study area in each sampling year. Plant abundance was quantified as: biomass (8 studies), point frame hits (total- 68 studies; top and bottom only- 15 studies; or top only- 14 studies), visual cover estimates (48 studies), subplot frequency (1 study), or stem counts (4 studies). Morphologically similar groups of taxa that were not consistently separated across all years of a given study were grouped to morphospecies (i.e. unknown moss) to permit temporal comparisons. Not every taxa or growth form category occurred or was measured at every study site or location, thus the sample sizes for vegetation

response groups vary. Height (cm) was also measured in 31 studies (10 locations), as the height of plants over a regular sampling grid in each study plot. The plant identity associated with each height was noted in 26 studies (8 locations). The full dataset has been archived at the Polar Data Catalogue².

Vegetation change indices:

Due to variability in species composition among studies, we used a hierarchical growth form classification scheme to compare vegetation change across studies. For each plot in each year in each study, we calculated the following response variables: abundance of each broad (shrubs, forbs, graminoids, mosses, and lichens) and narrow vascular growth form (deciduous shrubs; evergreen shrubs; dwarf (<15cm), low (15-50cm) and tall (>50cm) shrub species; grasses; rushes; and sedges); abundance of litter (attached and unattached dead plant material); Simpson diversity of vascular taxa; the mean canopy height; and the maximum height of each vascular plant growth form. We scored abundance using the original measurement units, which varied among studies. We used maximum rather than mean height for the taxa-specific height change measurements to minimize differences due to changes in the abundance of shorter or taller species. We used two approaches to create narrow growth form categories for shrubs, based on either leaf-longevity or taxa-specific height as reported in various flora since both traits appear to influence shrub response to summer temperature warming³. Fewer than 1/3 of studies identified mosses and lichens to species or subgroup, and these studies were highly clustered in the coldest regions (almost exclusively on permafrost). As a result, we did not analyze subgroups of mosses and lichens here. Diversity analyses included only studies which identified >95% of the total abundance of vascular plants to species. Similarly, studies were omitted from

the analysis of that growth form if unidentified vegetation comprised more than 5% of the potential abundance.

For each study, we calculated the direction of change in each vegetation response metric over time as the sign of the slope of a linear model of vegetation response variables versus time (e.g. total point frame hits/year). This metric is the most conservative analysis we could apply to the dataset, and assumes only that the direction of vegetation change detected would be the same regardless of the particular method used to quantify abundance (i.e. an increase in cover would also result in increase in biomass or point frame hits and vice versa). Such an approach has been used previously in a global synthesis of treeline advancement, wherein the methods used to detect change varied among studies⁴. Height change rates for each study were calculated based on the slope of a regression of height (cm) over time, yielding a change rate in cm/year.

We used generalized estimating equations (GEEs) to calculate biome-wide changes in vegetation height and abundance (population-averaged responses), specifying either a binomial or gaussian error structure. Marginal models were preferable to mixed-effects modeling in this study as we were primarily interested in population-averaged responses, not responses conditioned on random effects terms⁵. The response variable was the study-specific direction of abundance changes (binomial response variable), or the rate of change (cm/year, continuous response variable), an intercept was the single explanatory variable, and the location was included as a grouping factor with an exchangeable correlation structure. Significance was assessed using Wald tests.

Sources of environmental data:

3

We examined vegetation change in response to summer temperature change and interactions between summer temperature change and factors that have been previously shown to moderate plant response to summer climate warming^{3,6-10} for which reliable study-site specific data were widely available. The final suite of environmental variables we used included the summer (Jun-Aug or Dec-Feb) temperature change that occurred over the study period (Δ° C), summer (Jun-Aug or Dec-Feb) mean temperature (°C), presence of near surface permafrost (<1m active layer depth), and soil moisture class (dry, moist or wet). We used the monthly data provided at 0.5 degree resolution based on the University of East Anglia Climate Research Unit (CRU) TS3.1 dataset¹, with a lapse rate adjustment of -6° C/km elevation to account for differences in elevation between the actual study sites and the gridded data¹¹. These data extend through the year 2009. We also had local meteorological data for at least some years for $\sim 2/3$ of the studies, which we used to confirm the accuracy of the downscaled data. Based on the studies and years where both climate data sources were available, we confirmed that the absolute mean summer temperature estimates from the two sources were well correlated (Pearson r = 0.91), as were the interannual temperature anomalies (Pearson r=0.89). CRU data were not available for sub-Antarctic study site, so we used local meteorological station data for this study. We estimated mean summer temperature for each site over a common set of years (1996-2005), to provide inter-comparability among our datasets. We selected this decade because it overlaps with the majority of our sampling years, and because we lacked climate data from the site that lay outside the CRU map for other years. We classified each study by soil moisture class, with dry sites containing roughly <20% gravimetric soil moisture content (GMC); moist 20-60% GMC; or wet >60% GMC. Precipitation and snow are other potentially important factor in vegetation change. Unfortunately, relatively few sites had measured local precipitation or snow

duration, and the relationship between study-site specific data for these variables and gridded precipitation or snow cover datasets were weak. As a result, we did not use precipitation or snow data in our analyses.

Summer climate change index:

For each study, we determined summer temperature change (Δ° C) as follows: First, we calculated an annual rate of summer temperature change ($^{\circ}$ C/year) as the slope a linear regression of summer temperature on year over the relevant time period (first through last year of vegetation monitoring in each study). We then multiplied the annual rate of summer temperature change at each study by number years between the first and last survey year in each study to generate 158 study-specific estimates of total summer temperature change (Δ° C), corresponding to the relevant vegetation monitoring locations and timeframes.

Linking vegetation change to environmental conditions:

We used generalized estimating equations to test whether the direction of vegetation changes were correlated with local rates of summer climate warming. Based on previous reports of tundra vegetation sensitivity to summer climate warming, as well as differences in sensitivity to warming with ambient site temperature, over a soil moisture gradient, and on and off permafrost, we fitted four generalized estimating equations per vegetation response variable, with the following explanatory variables: summer temperature change; summer temperature change x mean summer temperature; summer temperature change x study site moisture; summer temperature change x permafrost. Main effects were also included in all models with interaction terms, and location was included as a grouping factor with exchangeable correlation structure. Since repeated tests could increase the probability of Type I errors, we present results (Table S2) with and without adjusting for the false discovery rate¹², but note this correction may be overly conservative, particularly since the explanatory variables were not entirely independent (studies with permafrost had lower mean summer temperatures than sites without). The single study conducted across a moisture gradient (RMBL from Table S1) was omitted from all tests that included soil moisture. We did not assess environmental correlates of change in plant height due to the low number of sites that measured heights. All analyses and plots were generated in R (version 2.11), with the packages geepack, doBy and ggplot2¹²⁻¹⁶.

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	tundra biome. Proc. Natl. Acad. Sci. U. S. A. 103, 1342-1346 (2006).
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	powerful approach to multiple testing. J. Roy. Statist. Soc. Ser. B 57, 289–300 (1995).
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Plot-scale evidence of tundra vegetation change and links to recent summer warming.

Table S1.

Study	Lat.	Long.	Elev.	Moisture	Perm.	Veg. Class	Sampling Metric	Years	P.I.	Reference
ABISKOWET	68.35	18.82	400	WET	N	W3	PFA	1999-2008	Michelsen	Rinnan et al. 2007; Unpubl data
PEATLAND	68.35	18.82	340	MOIST	Y	W3	PFA	2000-2008	Cornelissen	Keuper et al. 2011
GA66	65.59	-23.97	190	DRY	N	G3	COVER	1998-2005	Magnusson	Magnusson et al. 2005
MD72	65.51	-18.08	190	MOIST	Ν	G3	COVER	1998-2005	Magnusson	Magnusson et al. 2005
SB63	65.45	-18.24	370	DRY	N	G3	COVER	1998-2005	Magnusson	Magnusson et al. 2005
SY59	65.58	-19.84	320	DRY	Ν	G3	COVER	1998-2005	Magnusson	Magnusson et al. 2005
CASSIOPE BIOMASS	78.87	-75.67	30	MOIST	Y	P2	BIOMASS	1981-2007	Henry	Hudson & Henry 2009
CASSIOPE COVER	78.87	-75.67	30	MOIST	Y	P2	COVER	1981-2007	Henry	Hudson & Henry 2009
CASSIOPE ITEX	78.87	-75.92	30	MOIST	Y	P2	PFA	1995-2007	Henry	Hudson & Henry 2009
DOLOMITE COVER	78.88	-75.92	540	DRY	Y	B4	COVER	1992-2009	Lévesque	Levesque 1997; Unpubl. data
GRANITE COVER	78.88	-75.92	540	DRY	Y	B3	COVER	1992-2009	Lévesque	Levesque 1997; Unpubl. data
DOME.D ITEX	78.88	-75.92	540	DRY	Y	B4	PFA	1995-2008	Henry	Unpubl. data
DOME.G ITEX	78.88	-75.92	540	DRY	Y	B3	PFA	1995-2008	Henry	Unpubl. data
DRYAS	78.87	-75.67	30	MOIST	Y	G2	PFA	1995-2010	Henry	Unpubl. data
FERT	78.87	-75.67	30	MOIST	Y	P2	PFA	1995-2010	Henry	Unpubl. data
MEADOW BIOMASS	78.87	-75.67	30	WET	Y	W2	BIOMASS	1980-2005	Henry	Hill & Henry 2011
MEADOW ITEX	78.87	-75.67	30	WET	Y	W2	PFA	1995-2010	Henry	Unpubl. Data
WILLOW	78.87	-75.67	30	DRY	Y	P2	PFA	1995-2010	Henry	Unpubl. data
ATIGUN A	68.47	-149.35	1190	DRY	Y	P2	PFA	1997-2007	Jorgenson	Jorgenson et al. 2000; Unpubl. Data
ATIGUN B	68.48	-149.35	1210	MOIST	Y	G3	PFA	1997-2007	Jorgenson	Jorgenson et al. 2000; Unpubl. Data
ATIGUN C	68.45	-149.32	885	MOIST	Y	P2	PFA	1997-2007	Jorgenson	Jorgenson et al. 2000; Unpubl. Data
H1	69.66	-144.19	258	MOIST	Y	RS	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
Н3	69.85	-144.11	101	MOIST	Y	RS	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
H4	69.96	-144.06	43	DRY	Y	DT	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
Н5	69.95	-144.06	50	DRY	Y	DT	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
JAGO A	69.70	-143.63	198	MOIST	Y	G4	PFA	1996-2005	Jorgenson	Jorgenson et al. 1997; Unpubl. Data
JAGO B	69.71	-143.62	168	MOIST	Y	G3	PFA	1996-2005	Jorgenson	Jorgenson et al. 1997; Unpubl. Data
К2	70.08	-143.14	5	MOIST	Y	G3	PFA	1986-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
К3	70.08	-143.14	5	MOIST	Y	G3	PFA	1986-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
M10	69.80	-144.81	210	MOIST	Y	G4	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
M11	69.80	-144.81	214	MOIST	Y	G4	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
M4	69.79	-144.82	212	MOIST	Y	RS	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
M7S	69.80	-144.84	207	MOIST	Y	G4	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
N11	69.89	-142.87	83	MOIST	Y	G3	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
O11	69.97	-143.90	37	WET	Y	W2	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
012	69.97	-143.90	37	MOIST	Y	G3	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
013	69.83	-143.78	98	MOIST	Y	G3	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
O15	69.83	-143.77	101	MOIST	Y	RS	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data

Table S1 cont'd.

Study	Lat.	Long.	Elev.	Moisture	Perm.	Veg. Class	Sampling Metric	Years	P.I.	Reference
O18	69.97	-143.94	38	MOIST	Y	G3	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
O19	69.97	-143.94	38	MOIST	Y	G3	PFA	1985-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
O3	69.97	-143.91	36	MOIST	Y	G3	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
O6	69.98	-144.05	35	DRY	Y	DT	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
07	69.98	-144.02	32	MOIST	Y	G3	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
S1	69.70	-144.36	275	MOIST	Y	G4	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
S4	69.71	-144.37	232	MOIST	Y	S1	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
S5	69.71	-144.38	225	MOIST	Y	RS	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
S6	69.73	-144.34	202	MOIST	Y	S1	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
S8	69.73	-144.34	206	MOIST	Y	G4	PFA	1984-2009	Jorgenson	Jorgenson et al. 2010; Unpubl. data
AD	70.45	-157.41	22	DRY	Y	P2	PFTB	1997-2007	Hollister	Hollister et al. 2005; Unpubl. data
AW	70.45	-157.40	17	WET	Y	W2	PFTB	1997-2007	Hollister	Hollister et al. 2005; Unpubl. data
RATE BETULA SHRUB	70.46	-157.42	29	MOIST	Y	G4	COVER	2000-2009	Webber, Tweedie, Johnson	Unpubl. data
RATE CAREX WET MEADOW	70.46	-157.42	29	WET	Y	W2	COVER	2000-2009	Webber, Tweedie, Johnson	Unpubl. data
RATE DRYAS HEATH	70.46	-157.42	29	DRY	Y	P2	COVER	2000-2009	Webber, Tweedie, Johnson	Unpubl. data
RATE HIEROCHLOE DRY ME.	70.46	-157.42	29	DRY	Y	P2	COVER	2000-2009	Webber, Tweedie, Johnson	Unpubl. data
BETULAHEATH	65.27	-20.25	480	MOIST	N	S1	PFTB	1997-2007	Jónsdóttir	Jónsdóttir et al. 2005; Unpubl. data
BD	71.32	-156.60	5	MOIST	Y	G2	PFTB	1995-2008	Hollister	Hollister et al. 2005; Unpubl. data
BW	71.32	-156.60	3	WET	Y	W1	PFTB	1996-2008	Hollister	Hollister et al. 2005; Unpubl. data
MICRO MOIST MEADOW	71.29	-156.64	9	MOIST	Y	G3	COVER	1999-2008	Webber, Tweedie, Johnson	Unpubl. data
MICRO WETMEADOW	71.29	-156.64	9	WET	Y	G3	COVER	1999-2008	Webber, Tweedie, Johnson	Unpubl. data
ORD ARCTOPHILA POND	71.29	-156.64	9	WET	Y	W1	COVER	1999-2008	Webber, Tweedie, Johnson	Unpubl. data
ORD DRY HEATH	71.29	-156.64	9	DRY	Y	G2	COVER	1999-2008	Webber, Tweedie, Johnson	Unpubl. data
ORD CAREX MOIST MEADOW	71.29	-156.64	9	MOIST	Y	G3	COVER	1999-2008	Webber, Tweedie, Johnson	Unpubl. data
ORD CAREX MESIC MEADOW	71.29	-156.64	9	MOIST	Y	W1	COVER	1999-2008	Webber, Tweedie, Johnson	Unpubl. data
SD33	65.50	-20.23	350	MOIST	Ν	W2	COVER	1997-2005	Magnusson	Magnusson et al. 2005
SD34	65.50	-20.23	350	MOIST	Ν	W2	COVER	1997-2005	Magnusson	Magnusson et al. 2005
SHEEN B	68.57	-143.72	1002	MOIST	Ν	S2	PFA	1998-2008	Jorgenson	Jorgenson et al. 1997; Unpubl. Data
MESPOLYGON	73.23	-80.00	70	MOIST	Y	G2	PFA	2002-2008	Lévesque	Unpubl. data
MESPRAIRIE	73.23	-80.00	70	MOIST	Y	G2	PFA	2001-2008	Lévesque	Unpubl. data
AG4	65.78	-19.31	40	MOIST	Ν	G3	COVER	1997-2005	Magnusson	Magnusson et al. 2005
KD24	65.77	-19.04	180	MOIST	Ν	G3	COVER	1997-2005	Magnusson	Magnusson et al. 2005
KD25	65.77	-19.03	160	MOIST	Ν	W2	COVER	1997-2005	Magnusson	Magnusson et al. 2005
KNUTSHØ	62.30	9.62	1090	DRY	Ν	S1	COVER	1999-2008	Hofgaard	Hofgaard et al. 2010
RIDGE DRYAS HEATH	60.37	7.32	1550	MOIST	N	P1	SUBPLFREQ	2000-2008	Klanderud	Unpubl. data; Klanderud & Totland 2007
LH92	64.22	-20.60	80	WET	N	W2	COVER	1998-2005	Magnusson	Magnusson et al. 2005
SH90	63.98	-20.57	60	MOIST	N	G3	COVER	1998-2005	Magnusson	Magnusson et al. 2005
AH37	65.07	-20.58	450	MOIST	Ν	G3	COVER	1997-2005	Magnusson	Magnusson et al. 2005
AH38	65.08	-20.59	450	MOIST	Ν	G3	COVER	1997-2005	Magnusson	Magnusson et al. 2005
VH49	65.14	-20.26	400	MOIST	Ν	G3	PFTB	1997-2005	Magnusson	Magnusson et al. 2005

Table S1 cont'd.

Study	Lat.	Long.	Elev.	Moisture	Perm.	Veg. Class	Sampling Metric	Years	P.I.	Reference
KILPISJARVI	69.07	20.82	670	MOIST	Ν	S1	PFA	2003-2008	Tolvanen	Rinnan et al. 2009; Unpubl. data
PIKA	61.22	-138.27	1700	DRY	Y	G3	COVER	1996-2007	Koh, Hik	Unpubl. data
DRY HEATH	68.20	18.30	1000	DRY	Ν	S1	PFTB	1995-2008	Molau	Molau 1997; Unpubl. data
DRY MEADOW	68.20	18.30	1000	DRY	Ν	G3	PFTB	1996-2007	Molau	Bjork et al. 2007; Unpubl. data
TUSSOCK TUNDRA	68.20	18.30	1000	WET	Ν	G4	PFTB	1995-2006	Molau	Molau 2010
WET SEDGE	68.20	18.30	1000	WET	N	W1	PFTB	1994-2007	Molau	Molau 1997; Unpubl. data
BIS H	78.18	15.75	120	MOIST	Y	W1	PFA	2003-2009	Jónsdóttir	Unpubl. data
BIS L	78.18	15.75	100	MOIST	Y	W1	PFA	2003-2009	Jónsdóttir	Unpubl. data
CAS H	78.18	15.75	120	MOIST	Y	P2	PFA	2003-2009	Jónsdóttir	Unpubl. data
CAS L	78.18	15.75	100	DRY	Y	P2	PFA	2003-2009	Jónsdóttir	Unpubl. data
DRY H	78.18	15.75	120	DRY	Y	P1	PFA	2003-2009	Jónsdóttir	Unpubl. data
DRY L	78.18	15.75	100	DRY	Y	P1	PFA	2003-2009	Jónsdóttir	Unpubl. data
MES PHOTO	78.10	16.04	30	MOIST	Y	P2	COVER	2003-2008	Cooper	Cooper et al. 2006; Unpubl. data
WET PHOTO	78.10	16.04	25	WET	Y	W1	COVER	2003-2008	Cooper	Cooper et al. 2006; Unpubl. data
ALPINE SNOWBED	43.45	41.69	2750	MOIST	Ν	B3	SHTCNT (GEN)	1996-2009	Onipchenko	Unpubl. data
FVG LOW	43.45	41.69	2710	MOIST	Ν	B3	SHTCNT	1986-2009	Onipchenko	Unpubl. data
FVG UPPER	43.45	41.69	2710	MOIST	Ν	B3	SHTCNT	1987-2009	Onipchenko	Unpubl. data
LICHEN HEATH	43.45	41.69	2750	MOIST	Ν	B3	SHTCNT	1981-2008	Onipchenko	Unpubl. data
LH69	65.94	-18.11	90	MOIST	Ν	W2	COVER	1998-2005	Magnusson	Magnusson et al. 2005
MV51	65.78	-18.27	160	MOIST	Ν	W2	COVER	1998-2005	Magnusson	Magnusson et al. 2005
MV52	65.77	-18.28	160	MOIST	Ν	G3	COVER	1998-2005	Magnusson	Magnusson et al. 2005
BARREN SADDLE	40.05	-105.58	3528	DRY	Ν	B1	PFT	1989-2006	Spasojevic	Walker et al. 1994; Unpubl. data
DRY MEADOW SADDLE	40.05	-105.58	3528	DRY	Ν	B4	PFT	1989-2006	Spasojevic	Walker et al. 1994; Unpubl. data
FELLFIELD SADDLE	40.05	-105.58	3528	DRY	Ν	B4	PFT	1989-2006	Spasojevic	Walker et al. 1994; Unpubl. data
KLEIN	40.05	-105.60	3500	MOIST	Ν	G1	PFA	1993-2000	Walker, Klein	Walker et al. 1994; Unpubl. data
MOIST MEADOW SADDLE	40.05	-105.58	3528	MOIST	Ν	G1	PFT	1989-2006	Spasojevic	Walker et al. 1994; Unpubl. data
ORD. DRY MEADOW	40.05	-105.58	3505	DRY	Ν	B4	COVER	1991-2001	Ebert-May, Tweedie, Johnson	Unpubl. data
ORD. FELLFIELD	40.05	-105.58	3505	DRY	Ν	B4	COVER	1991-2001	Ebert-May, Tweedie, Johnson	Unpubl. data
ORD. MOIST MEADOW	40.05	-105.58	3505	MOIST	Ν	G1	COVER	1991-2001	Ebert-May, Tweedie, Johnson	Unpubl. data
ORD. MOIST SHRUB	40.05	-105.58	3505	MOIST	Ν	S2	COVER	1991-2001	Ebert-May, Tweedie, Johnson	Unpubl. data
ORD. WET MEADOW	40.05	-105.58	3505	WET	Ν	W1	COVER	1991-2001	Ebert-May, Tweedie, Johnson	Unpubl. data
ORD. SNOWBANK	40.05	-105.58	3505	WET	Ν	W1	COVER	1991-2001	Ebert-May, Tweedie, Johnson	Unpubl. data
SNOWBANK SADDLE	40.05	-105.58	3528	WET	N	W1	PFT	1989-2006	Spasojevic	Walker et al. 1994; Unpubl. data
WET MEADOW SADDLE	40.05	-105.58	3528	WET	Ν	W1	PFT	1989-2006	Spasojevic	Walker et al. 1994; Unpubl. data
SA16	65.47	-18.70	580	MOIST	Ν	G3	COVER	1997-2005	Magnusson	Magnusson et al. 2005
SA17	65.47	-18.69	590	MOIST	Ν	G3	COVER	1997-2005	Magnusson	Magnusson et al. 2005
SA19	65.48	-18.90	510	MOIST	Ν	G3	COVER	1997-2005	Magnusson	Magnusson et al. 2005
COPECK G	-36.90	147.27	1690	DRY	Ν	S1/S2	PFA	1988-2002	Wahren	Unpubl. data
COPEHUT G	-36.90	147.27	1690	DRY	Ν	S1/S2	PFA	1985-2002	Wahren	Unpubl. data
CULTIVATION G	-36.90	147.27	1680	DRY	Ν	S1/S2	PFA	1985-1998	Wahren	Unpubl. data

Table S1	cont'd.

Study	Lat.	Long.	Elev.	Moisture	Perm.	Veg. Class	Sampling Metric	Years	P.I.	Reference
EASTBASE G	-36.90	147.27	1645	DRY	Ν	S1/S2	PFA	1989-1998	Wahren	Unpubl. data
FAINTER G	-36.90	147.27	1770	DRY	Ν	S1/S2	PFA	1989-1998	Wahren	Unpubl. data
JOHNSTONS G	-36.90	147.27	1750	DRY	Ν	S1/S2	PFA	1992-1998	Wahren	Unpubl. data
PV NEW G	-36.90	147.27	1750	DRY	Ν	S1/S2	PFA	1992-1998	Wahren	Unpubl. data
PV OUT G	-36.90	147.27	1750	DRY	Ν	S1/S2	PFA	1989-1999	Wahren	Unpubl. data
TADGELL G	-36.90	147.27	1900	DRY	Ν	S1/S2	PFA	1989-1998	Wahren	Unpubl. data
HE	69.58	-138.86	76	MOIST	Y	G4	PFA	1999-2009	Myers-Smith	Myers-Smith et al. 2011; Unpubl. data
KO	69.58	-138.87	73	DRY	Y	P1	PFA	1999-2009	Myers-Smith	Myers-Smith et al. 2011; Unpubl. data
RMBL	37.95	-106.98	2920	MIXED	Ν	S1/S2	BIOMASS	1991-2005	Harte	Harte et al. 2006
TUNDRA	-64.78	-64.07	30	MOIST	Ν	S1	COVER	1996-2006	Day	Day et al. 2008; Unpubl. data
SVERDRUP	79.14	-79.62	461	DRY	Y	P1	COVER	1992-2009	Levesque	Levesque 1997; Unpubl. data
F1	43.54	142.87	1710	DRY	Ν	S1	PFA	2002-2007	Kudo	Kudo et al. 2010
F2	43.55	142.86	1910	DRY	Ν	P2	PFA	2002-2007	Kudo	Kudo et al. 2010
S1	43.55	142.87	1820	MOIST	Ν	G3	PFA	2002-2007	Kudo	Kudo et al. 2010
S2	43.55	142.86	1820	MOIST	Ν	G3	PFA	2002-2007	Kudo	Kudo et al. 2010
MOSS HEATH	64.28	-21.08	120	DRY	Ν	MH	PFTB	1996-2007	Jónsdóttir	Jónsdóttir et al. 2005; Unpubl. data
PALSA	64.57	-18.60	600	DRY	Y	G2	PFA	1984-2007	Thorhallsdottir	Unpubl. data
SALIXHEATH	64.57	-18.60	600	DRY	Ν	S1	PFA	1984-2007	Thorhallsdottir	Unpubl. data
HH100	63.56	-20.17	5	MOIST	Ν	G3	COVER	1998-2005	Magnusson	Magnusson et al. 2005
RT81	63.99	-21.16	30	MOIST	Ν	G3	COVER	1998-2005	Magnusson	Magnusson et al. 2005
VE82	63.97	-21.17	15	MOIST	Ν	W2	COVER	1998-2005	Magnusson	Magnusson et al. 2005
DRY ITEX	68.63	-149.59	720	DRY	Y	P2	PFTB	1994-2007	Gould	Wahren et al. 2005; Unpubl. Data
IMNAVAIT GRID	68.61	-149.61	899	MOIST	Y	G4	PFTB	1989-2007	Gould	Unpubl. data
LTER HEATH	68.60	-149.60	745	DRY	Y	P2	BIOMASS	1996-2006	Shaver	Gough et al. 2002; Unpubl data
LTER MOIST ACIDIC TUSS.	68.60	-149.60	745	MOIST	Y	G4	BIOMASS	1999-2006	Shaver	Hobbie et al. 2005; Unpubl data
LTER WETSEDGE	68.60	-149.60	745	WET	Y	W1	BIOMASS	1994-2001	Shaver	Shaver et al. 1998; Unpubl. data
MOIST ITEX	68.63	-149.59	720	MOIST	Y	P2	PFTB	1994-2008	Gould	Wahren et al. 2005; Unpubl. data
SAG WETSEDGE2	68.60	-149.60	745	WET	Y	W1	BIOMASS	1988-2001	Shaver	Shaver et al. 1998; Unpubl. data
TUSSOCK 1981PLOTS	68.63	-149.58	745	MOIST	Y	G4	BIOMASS	1982-2000	Shaver	Shaver et al. 2001; Unpubl. data
TUSSOCK GRID	68.62	-149.61	731	MOIST	Y	G4	PFTB	1990-2008	Gould	Unpubl. data
ALPINE	46.47	9.58	2490	MOIST	Ν	G2	COVER	1994-2009	Rixen	Gugerli 1997; Unpubl. data
WOLFCREEK	61.56	-135.13	1526	DRY	Ν	P1	PFA	1998-2008	Loewen, Johnstone	Pieper et al. 2011
ABRASION PLATEAU	74.29	-20.31	80	DRY	Y	B1	PFT	1997-2008	Schmidt	Schmidt et al. In review
CASSIOPE HEATH	74.28	-20.33	35	MOIST	Y	P2	PFT	1997-2008	Schmidt	Schmidt et al. In review
DRYAS HEATH	74.29	-20.29	150	DRY	Y	P1	PFT	1997-2008	Schmidt	Schmidt et al. In review
FEN	74.28	-20.33	30	WET	Y	W1	PFT	1997-2008	Schmidt	Schmidt et al. In review
GRASSLAND	74.28	-20.33	45	MOIST	Y	W1	PFT	1997-2008	Schmidt	Schmidt et al. In review
OPEN DRYAS VEGETATION	74.28	-20.31	30	DRY	Y	P1	PFT	1997-2008	Schmidt	Schmidt et al. In review
SALIX ARCTICA SNOWBED	74.28	-20.32	45	MOIST	Y	P1	PFT	1997-2008	Schmidt	Schmidt et al. In review
VACCINIUM HEATH	74.28	-20.38	10	MOIST	Y	P2	PFT	1997-2008	Schmidt	Schmidt et al. In review

Table S1. Study details. Lat - Latitude(°N); Long - Longitude (°E); Elev - Elevation(m); Perm - and presence of near-surface permafrost (Y=Yes, N=No); Sampling metric (BIO= Biomass, PFA= Point frame all hits, PFTB = Point frame top bottom hits only, PFT = Point frame top hits only, COV= Cover, SHTCT = count of all or generative only (GEN) shoots, SUBLFREQ= subplot frequency); Vegetation type (based on CAVM classes wherever possible, see Walker *et al* 2005 for detailed descriptions: B1=Cryptogam, herb barren; B3=Noncarbonate mountain complex; B4=Carbonate mountain Complex; DT=Riparian terrace (Dryas-dominated); G1=Rush/grass, forb, cryptogam tundra; G2 = Graminoid, prostrate dwarf-shrub, forb tundra; G3=Non-tussock sedge, dwarf-shrub, moss tundra; G4=Tussock-sedge, dwarf-shrub, moss tundra; MH= Moss heath; P1=Prostrate dwarf-shrub, herb tundra; S2=Low-shrub tundra; W1=Sedge/grass, moss wetland; W2=Sedge, moss, dwarf-shrub wetland; W3=Sedge, moss, low-shrub wetland); Years - first and last years of study; P.I. - Principle Investigator of study; Reference - recent study site publication, if applicable.

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Table S2.

Response Group	Δ°C	$\Delta^{\circ}C \times Mean^{\circ}C$	$\Delta^{\circ}C \times Perm$	$\Delta^{\circ}C$ x Moisture
LITTER	0.100	0.934	0.287	0.115
DIVERSITY (VASC)	0.682	0.485	0.081	0.543
BARE GROUND	0.241	0.818	0.458	0.332
SHRUB(TOTAL)	0.105	0.015	0.200	0.083
DECIDUOUS	0.361	0.006*	0.245	0.031
EVERGREEN	0.155	0.178	0.737	0.264
DWARF	0.349	0.298	0.910	0.751
LOW	0.042	0.504	0.233	0.844
TALL	0.041	0.175	0.446	0.874
GRAMINOID(TOTAL)	0.828	0.130	0.130	0.156
GRASS	0.910	0.127	0.205	0.424
RUSH	0.320	0.325	0.212	0.047
SEDGE	0.587	0.086	0.698	0.128
FORB(TOTAL)	0.379	0.292	0.012*	0.290
LICHEN(TOTAL)	0.175	0.322	0.510	0.140
MOSS(TOTAL)	0.216	0.412	0.111	0.971

Table S2. Wald test results (*P* values) correlating temporal changes in vegetation response groups to hypothesized drivers of change: summer temperature change (Δ° C) and interactions between summer temperature change and mean summer temperature (Δ° C x Mean^oC); presence of near surface permafrost (Δ° C x Perm); and soil moisture class Δ° C x Moisture). Bold indicates significance at *P*<0.05, stars indicate significance at *P*<0.05 after accounting for multiple tests.