

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

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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, plot-based 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 ecosystems^{9–13}. 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 °C (standard error (s.e.m.) = 0.10); $p < 0.0001$ based on generalized estimating equations (GEEs), range = –1.47–2.29 °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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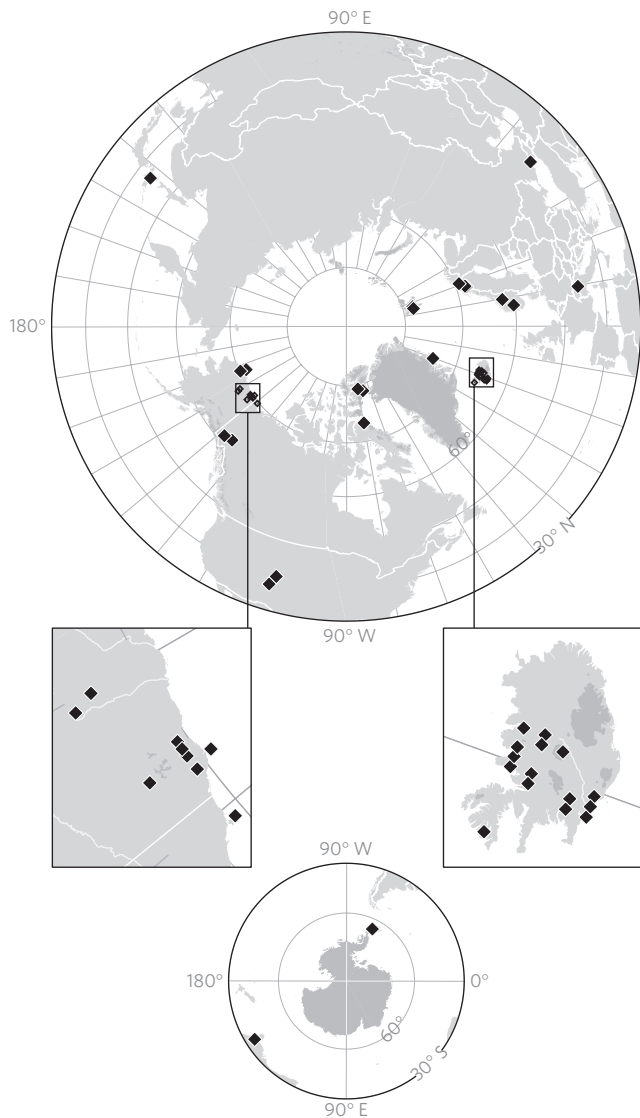


Figure 1 | Study site locations. Study sites spread across the tundra biome in the Arctic, alpine and Antarctic regions. Black symbols represent the grid-cell centres of the 46 locations into which the 158 studies were grouped for the analysis.

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

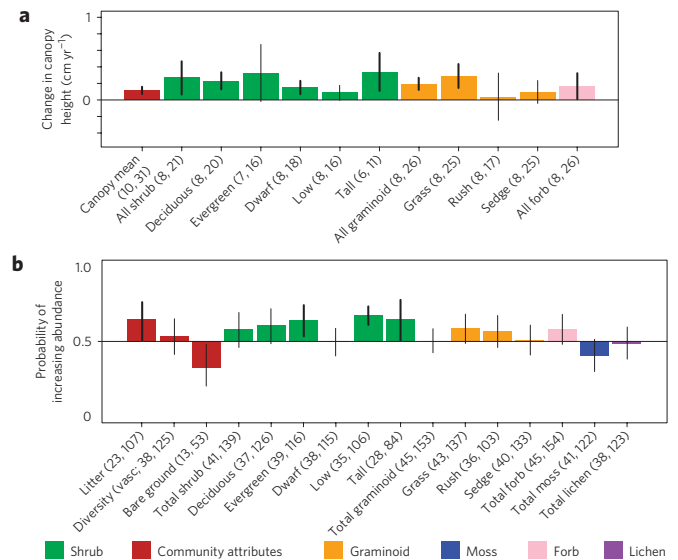


Figure 2 | Biome-wide changes in vegetation height and abundance.

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 near-surface 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 well-documented 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

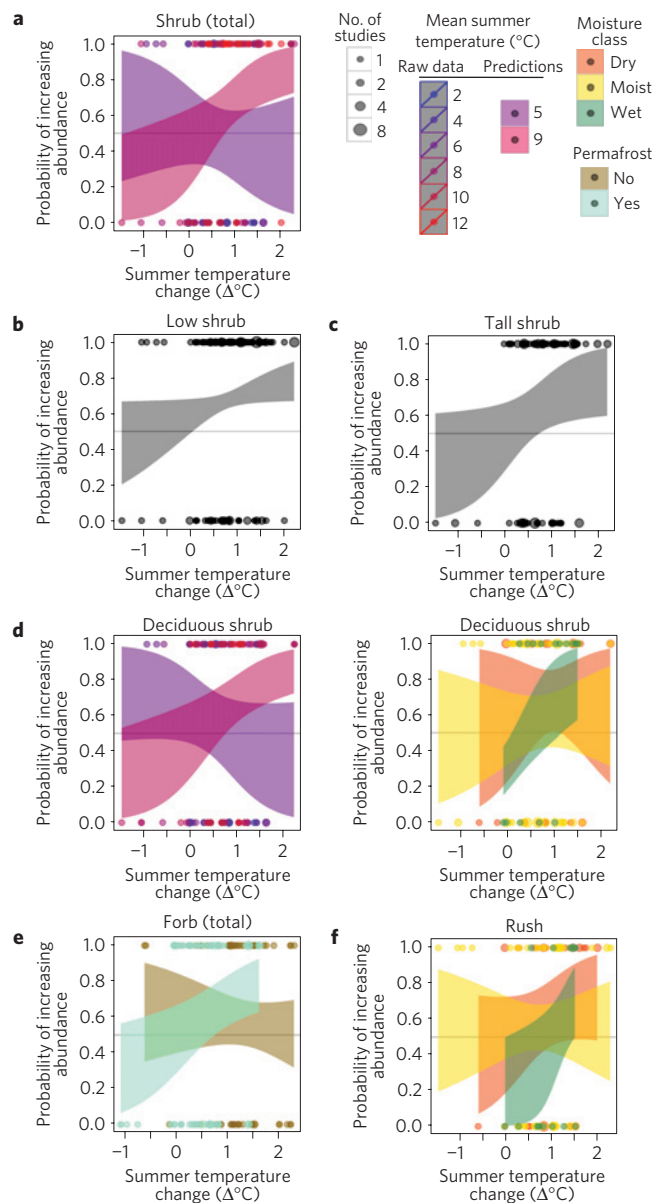


Figure 3 | Relationship between vegetation change and summer temperature change. Vegetation change as a function of summer temperature change. **a–f**, Bands show the predicted probability of increase ± 2 s.e.m., based on GEEs where the change in vegetation response groups was significantly correlated 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, growing-season 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

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 ($\Delta^\circ\text{C}$) 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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